ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

Published by the
ENTOMOLOGICAL SOCIETY OF AMERICA
Formed in 1953 by Consolidation of the
American Association of Economic Entomologists
(1889-1952)
and the former
Entomological Society of America
(1906-1952)

Volume 51 May, 1958 Number 3

ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

THE ENTOMOLOGICAL SOCIETY OF AMERICA
1530 P Street, N. W.
Washington 5, D. C.

ROLAND F. HUSSEY, *Editor*
University of Florida,
Gainesville, Florida

EDITORIAL BOARD

R. I. SAILER, *Chairman*, Washington, D. C. (A, 1958)
M. H. HATCH, Seattle, Wash. (A, 1959)
L. E. ROZEBOOM, Baltimore, Md. (D, 1960)
J. A. ADAMS, Poughkeepsie, N. Y. (C, 1961)
J. J. PRATT, Wayland, Mass. (B, 1962)

A bimonthly journal published on the 15th of January, March, May, July, September, November, devoted to the interest of classical entomology. Authors are entirely responsible for statements in the *Annals*, whether of fact or opinion.

TERMS OF SUBSCRIPTION. Non-members in North America and U. S. Possessions—$12.00 per year; elsewhere—$12.00 plus 60¢ postage. Single copies $2.25, plus postage of 10¢ per copy. Deliveries overseas are not guaranteed and foreign mailings are made at the subscriber's risk.

LOST NUMBERS. Missing numbers cannot be supplied free of charge unless notice is received within 60 days after the appearance of issues concerned.

BACK NUMBERS are furnished at the following prices: volumes 1 to 31, $4.00 per volume, $1.00 per issue; volumes 32 to 38, $5.00 per volume, $1.25 per issue; volumes 39 to 45, $6.00 per volume, $1.50 per issue; volumes 46 to 48, $10.00 per volume, $2.50 per issue, volume 49 and 50, $12.00, $2.25 per issue.

REPRINTS. No gratis copies are supplied. A schedule of prices which will apply to orders received before the Annals is printed, and an order form are sent with proof. For price schedule, see Bulletin of the Entomological Society of America, Vol. 1, No. 4, December, 1955, or page 509 of Vol. 49(5) of the *Annals*.

BUSINESS COMMUNICATIONS of the Society and **SUBSCRIPTIONS AND MATTERS PERTAINING TO ADVERTISEMENTS** should be sent to the Executive Secretary, Entomological Society of America, 1530 P Street, N. W., Washington 5, D. C. Change of address must reach the office of the Executive Secretary 5 days prior to the month of issue to be effective for that month. Members should make use of the postal regulations which provide for forwarding of second class mail if postage upon delivery is guaranteed.

POSTAL EMPLOYEES send notice on Form 3579 to 1530 P Street, N.W., Washington 5, D.C.

MANUSCRIPTS and other copy for the Annals should be addressed to the Editor. Prompt publication of acceptable matter may be secured by payment of the cost of printing and engraving ($16.00 per page plus cost of engravings with additional charge for excessive tabular matter). Cost of engravings in excess of $15.00, for each eight printed pages or major fraction thereof, will be charged to the author. Before preparing manuscripts for publication in the Annals, authors are urged to consult the Publication Policies and Manuscript Rules and Suggestions given in Vol 49(5): 506–9, September 1956.

THE THOMAS SAY FOUNDATION. Five volumes have been published. Send inquiries and orders to Executive Secretary, Entomological Society of America, 1530 P Street, N. W., Washington 5, D. C.

Entered as second class matter April 11, 1908, at the Post Office at Columbus, Ohio, under the act of Congress of March 3, 1879. Subject to rate of postage provided for in Paragraph 4, Section 538, P. L. & R., authorized September 16, 1940

Printed by The Spahr & Glenn Company,
50 East Broad Street
Columbus 15, Ohio, U. S. A.

Issued May 15, 1958

Annals of
The Entomological Society of America

Volume 51 MAY, 1958 No. 3

A REPORT ON HAEMAGOGUS MOSQUITOES IN THE UNITED STATES WITH NOTES ON IDENTIFICATION (DIPTERA: CULICIDAE)[1]

OSMOND P. BRELAND[2]
The University of Texas, Austin

ABSTRACT

During the 1956 and 1957 approximately 190 collections were made from tree holes along the Texas-Mexico border between Brownsville and El Paso in search of *Haemagogus equinus* Theobald. This jungle mosquito, a known vector of the yellow fever virus, has only recently been reported from the United States. Tree-hole breeding mosquitoes of several species were recovered in 55 of the collections but *H. equinus* was found only six times (three times in one cavity) and only in the Brownsville region, where other workers have also recorded this species. It seems well established in the Brownsville area but its population is probably small as compared with those of other tree-hole mosquitoes. Several larvae were collected that may represent a species other than *H. equinus*. Methods of distinguishing *H. equinus* from other mosquitoes in this country are discussed, and a key is included for all mosquito larvae known to occur in tree holes in the eastern half of the United States. Additional studies are necessary before positive conclusions can be drawn regarding the possible future status and importance of *Haemagogus* mosquitoes in this country.

INTRODUCTION

Several species of so-called jungle mosquitoes of the genus *Haemagogus* have been established as being of considerable importance in the epidemiology of yellow fever. None of these mosquitoes were known to occur in the United States until a short time ago, when *Haemagogus equinus* Theobald was collected near Brownsville, Texas (Trapido and Galindo, 1956). This species bites man (Levi-Castillo, 1951), it has transmitted the yellow fever virus in the laboratory, and the virus was recently recovered from specimens collected in nature (Rondaniche and Galindo, 1957).

Various factors which favor the possibility that the yellow fever virus might be reintroduced into the United States have been noted on numerous occasions (e.g. Soper, 1955; Elton, 1956; Breland, 1957a). Since the presence of *H. equinus* in this country is one of these factors, the writer and his associates have recently been working to determine the status of these mosquitoes in the United States. One objective of this paper is to give a progress report of our work and that of other known workers to date. Another objective is to indicate how *Haemagogus equinus* may be distinguished from other mosquitoes in this country with which it is most likely to be associated. It is hoped that the inclusion of a key to the larvae of tree-hole breeding mosquitoes in the eastern half of the United States will be of assistance in this connection.

THE PRESENT STUDY

It is well known that *Haemagogus* mosquitoes breed primarily in tree holes containing water and for this reason these sites have been emphasized in the investigations. The collection of immature stages rather than adults has been emphasized, since as has been pointed out previously (Breland, 1954) many more of the former can be found routinely in a limited time. We have, however, used a portable light trap on several occasions, and have sat quietly for long periods in areas from which *Haemagogus* larvae have been collected. To date no adults of this species have been found. The equipment and the methods used in this work were essentially the same as those described in a former paper (Breland, 1957b).

During 1956 and 1957 we have made collections

[1]This investigation was supported and partial cost of publication of this paper was met by the Research and Development Division, Office of the Surgeon General, Department of the Army, under contract No. DA-49-007-MD-744. Accepted for publication January 28, 1958.

[2]Thanks are due to the following who assisted in the work herein outlined: John Riemann, Fred Klaus, Robert Sluss, and Dr. James Long; and to Jane Hubby who made the drawings.

from Brownsville, at the southern tip of Texas, along the Texas-Mexico border to El Paso, a distance of more than 800 miles. These collections have included more than 100 cavities and approximately 190 individual collections. Tree-hole breeding mosquitoes of one kind or another have been recovered from 55 of these collections, but *H. equinus* has been found only six times. All recoveries of this species have been made in the vicinity of Brownsville, Texas. Three of the collections of *H. equinus* were made from the same cavity in a hackberry tree (*Celtis* sp.) in April, June, and July of 1957.

During this work collections have been made from many species of trees, but so far *H. equinus* has been recovered from only two. These are the hackberry noted above, and Texas ebony (*Pithecolobium flexicaule*). None of these mosquitoes have ever been found in isolated trees, but all collections have been made in areas of rather dense vegetation. With one exception the cavities have been less than 6 feet above the ground and with a relatively small opening. This one exception is the hackberry from which *H. equinus* has been recovered on three different occasions. This cavity has an opening approximately 7 inches in diameter, is about 12 inches deep, and 7 feet above the ground. Dense vegetation surrounds the opening of this hole, and it is suggested that the amount of light may be a factor in determining the desirability of a breeding site for this species. No series of pH readings has as yet been made, but on one occasion *H. equinus* larvae were found in water with a pH of 8.3.

To date only small numbers of *H. equinus* larvae have been found, and this species often represents a relatively small percentage of the total population of mosquito larvae that occur in a given cavity. For example, in one collection of 215 larvae only 9 were *H. equinus*; in another of 158 larvae, 3 were this species.

DISCUSSION

The data which we and other workers have so far accumulated are not as yet sufficient for us to base any positive conclusions relative to the ultimate status and significance of *H. equinus* in the United States. Many of the collections were made during periods of drouth, and only one collection has been made from several of the localities. However, a few tentative suggestions or speculations might be appropriate at this time. These include the following.

First, *Haemagogus equinus* seems well established in the region of Brownsville, Texas. Since the species was first reported from this area at least one additional record has been published (Eads and Strom, 1957), and other workers have stated to the writer that they have also collected this species. This mosquito, including the recoveries reported in the present paper, has thus been collected on 10 to 15 separate occasions. There are three general collection localities known to us and these form a triangle approximately 10 miles on each side. The recovery of this species three different times from the same cavity also seems to indicate that it is well established in the area.

A second suggestion is that the population of *H. equinus* is not as yet very large in the Brownsville area. This suggestion is based upon the small number of this species that has been found in a relatively large number of collections. We have collected from more than 60 cavities in the region and many of these have been checked several times. *Haemagogus equinus* has been recovered from only four of these tree holes, and as indicated previously, the number of specimens has been relatively few. Other workers have doubtless examined many additional sites with the same general results (e.g. Eads and Strom, 1957). Additional collections during periods of rain, however, will be necessary before this suggestion can be confirmed.

A third postulate is that *H. equinus* prefers cavities in relatively dense vegetation, and unless a change of habit occurs isolated trees are not likely to be important breeding sites. All collections of this species known to the writer have been made in this type of habitat, and the openings of the cavities are either small or surrounded by dense vegetation.

DISTINGUISHING FEATURES OF *Haemagogus equinus*

It has been mentioned previously that we have never collected adult *equinus*, and so far as can be determined, no one else has collected the adults in the United States. In the event this should occur, these mosquitoes upon superficial examination are most likely to be confused with certain species of *Psorophora* than with any other mosquito known to occur in the area. Both differ from other endemic species in that areas of the body are covered with metallic greenish or bluish scales. However, aside from technical differences, *H. equinus* can also be distinguished from the *Psorophora* on the basis of color alone. Except for *P. cyanescens* (Coq.), other *Psorophora* in this region with metallic coloration have at least one white hind tarsal segment; all tarsal segments of *H. equinus* are dark. Greenish or bluish scales cover large areas of the occiput and the scutum in *equinus*, whereas in *P. cyanescens*—as well as in the other metallic *Psorophora*—most of the scales of these areas are yellowish, whitish, and/or brownish.

All past experience indicates that future workers are much more likely to collect larvae of *H. equinus* than adults, and hence the problem of distinguishing the larvae is probably of more current significance. In addition to *H. equinus*, eight other species of mosquitoes in Texas are known to breed routinely in tree holes. These

are *Orthopodomyia alba* Baker, *O. signifera* (Coq.), *Toxorynchites rutilus septentrionalis* (D. and K.), *Anopheles barberi* Coq., *Aedes triseriatus* (Say), *A. zoosophus* D. and K., *A. thibaulti* D. and K., and a member of the *Aedes muelleri* complex. This last named species has only recently been reported from Texas. (Breland, MS).

In addition to species that routinely breed in tree holes, several other species have been recovered occasionally from these situations. We have collected *Culex quinquefasciatus* Say, *C. restuans* Theob., and *Culiseta inornata* (Williston) from tree holes, and *Aedes atropalpus* (Coq.) has been recovered by Hedeen (1953). In addition *Anopheles punctipennis* (Say), *Aedes aegypti* (L.), and *Culex apicalis* Adams are reported by Jenkins and Carpenter (1946). This latter species we believe to be *Culex territans* Walker, since the report was made before the revision of this species

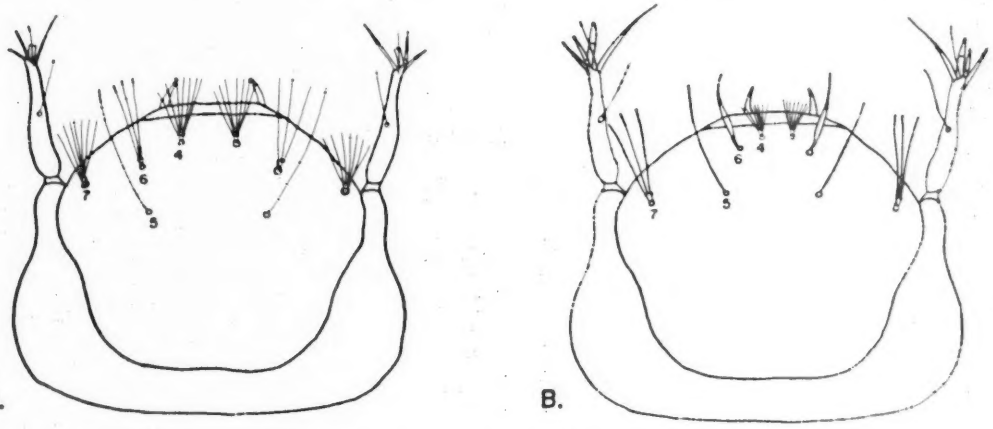


FIG. 1.—Heads of mosquito larvae, dorsal view, showing distinguishing features. A. *Aedes triseriatus* (Say). B. *Haemagogus equinus* Theobald.

group by Bohart (1948). Obviously, those species that breed primarily in cavities are most likely to be found with *H. equinus*, but all must be considered as being potential associates.

It is well known to mosquito taxonomists that there are generic key features by which the larvae of most genera in the United States can be distinguished from each other. This is not true, however, with respect to the larvae of *Aedes* and *Haemagogus*. The larvae of these two genera are therefore more difficult to differentiate than are the larvae of the other genera that breed in tree holes. For this reason, and because so far only *Aedes* larvae have been found with *H. equinus*, species of *Aedes* will be emphasized in the discussion that follows. However, all species listed herein are included in the key.

To date, *Aedes triseriatus* and *A. zoosophus* are the only species of mosquitoes that have been found associated with *H. equinus*. If placed in clear water, the larvae of the two latter species can often be distinguished with the unaided eye; *A. zoosophus* is white in color, whereas, *H. equinus* is dark. In the event workers prefer to examine the living larvae with a binocular microscope, the two can be differentiated by using the same features as those discussed in more detail with respect to *A. triseriatus*. *A. zoosophus* and *A. triseriatus* are essentially the same so far as the features used for this purpose are concerned. On permanently mounted slides, *A. zoosophus* can be identified by the presence of a light-colored hole or depression near the ventral margin of the saddle (Breland, 1949), a characteristic that does not occur in any other species in the United States so far as known.

Larvae of *A. triseriatus* are dark, and consequently they cannot be distinguished from *H. equinus* on the basis of color alone. It is possible, however, to distinguish these two species even in the living state by the use of a dissecting microscope (Fig. 1). Several minor differences in the heads of the two species occur, but the outstanding difference is in head hair 6, the lower head hair. In *H. equinus* this hair is coarse and single, but in *A. triseriatus* it is fine and with two or more branches. By the use of color and this feature the writer has successfully separated three living *H. equinus* larvae from a mixed culture of more than 150 *A. zoosophus* and *A. triseriatus*. All remaining larvae were killed to check the accuracy of this feature. This characteristic is also obviously of value in a study of mounted slides.

Additional differences occur in the terminal segments of the larvae (Fig. 2). The most easily seen distinction is that *A. triseriatus* (Fig. 2.A) has one or more preeratal tufts, that is, tufts in the ventral brush anterior to the barred area. All the tufts in *H. equinus* are confined to the barred area. A good comparative difference, once a person has seen it, is the relative length

of the spicules or denticles on the dorsal posterior region of the saddle. Some *triseriatus* larvae have no obvious spicules, but others as indicated in figure 2,A have some that are easily seen. In all specimens examined, however, these denticles are much longer and more obvious in *H. equinus*. These denticles can often be seen in living larvae with a dissecting microscope, but since the feature is a comparative one, it is much more valuable to a worker after he has seen the situation in both species. In the experience of the writer, the head hair feature is a much more rapid and accurate method of spotting living *H. equinus* larvae when mixed with *A. triseriatus*.

At the present time, the species of the *A. muelleri* complex mentioned previously is known only from one locality which is nineteen miles south of Alpine in west Texas. This is several hundred miles west of the region from which *H. equinus* is known, but it has been predicted that *H. equinus* will be found in the same general area (Trapido in Soper, 1955). The writer has seen the larvae of both species in the living state, but has never seen them together; consequently the suggested differences in living larvae are based upon examinations at different times rather than upon an actual comparison.

The larvae of *A. muelleri* seen by the writer are about as white as those of *A. zoosophus*, and it is believed that in clear water these larvae could be distinguished from the darker *H. equinus* on the basis of color. In the event the color distinction should not be sufficient, it is probable that the separation of these living larvae would be more difficult than if *A. triseriatus* were involved, since head hair 6 in *A. muelleri* is also single. However, it is finer than this hair in *H. equinus*, and it seems likely that this feature plus the more obvious denticles on the saddle of *H. equinus* should prove sufficient means for separation of the two.

Mounted slides of *A. muelleri* and *H. equinus* are easily distinguished. *A. muelleri* has one or more precratal tufts in the ventral brush, and the larger denticles of *H. equinus* are quite obvious under the compound microscope.

So far as present knowledge is concerned, the larvae of *Aedes thibaulti* are found primarily in bases of sweetgum and tupelo-gum trees that are subjected to flooding. It may be that *H. equinus* will never be found in this type of breeding habitat, but if so, the two species should not be difficult to distinguish. The writer has never examined carefully living larvae of *A. thibaulti*, but it seems probable that these should be very easy to differentiate even in the living state. Head hair 5 or the upper head hair in *A. thibaulti* is multiple as opposed to the single hair in *H. equinus* and in the other *Aedes* under discussion. Head hair 6 also has from two to five branches. The comb scales of *A. thibaulti* are arranged in a triangular patch, a distinction easily seen on a mounted slide.

During the course of this study several larvae have been collected which vary considerably from the accepted description of *H. equinus*. Head hair 6 of these larvae is double and the lateral hair of the anal segment (hair 1) has four to six branches. The writer has not examined living larvae of this type, but the branches of

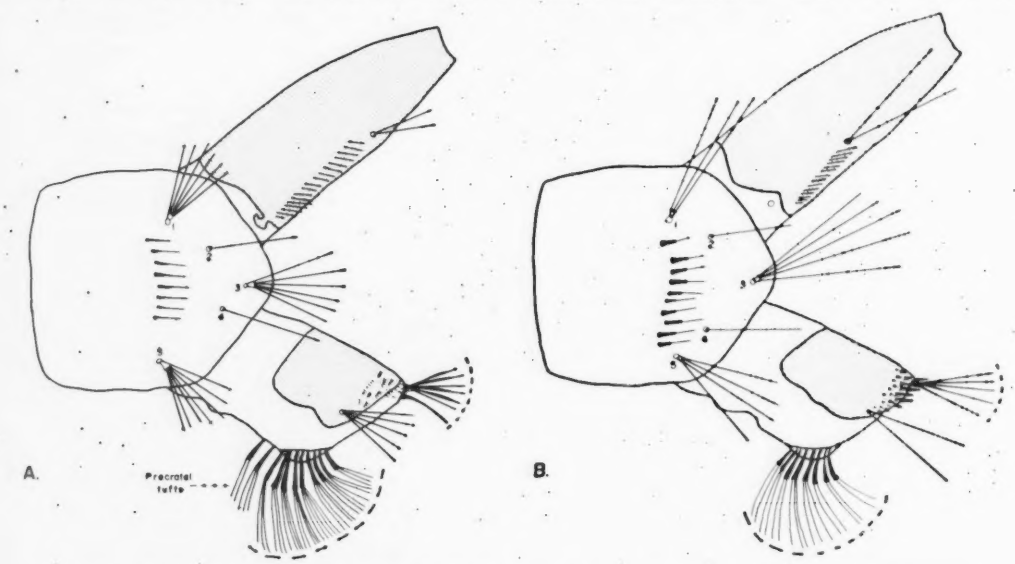


FIG. 2.—Terminal abdominal segments of mosquito larvae, lateral view, showing distinguishing features. A, *Aedes triseriatus* (Say). B, *Haemagogus equinus* Theobold.

hair 6 are coarser than those of *A. triseriatus* and this feature plus the large denticles of the saddle should make it possible to differentiate living larvae of the two species. These larvae either represent a different species or the larvae of *H. equinus* are considerably more variable than published descriptions indicate. Larger series of larvae as well as reared adults must be obtained before this problem can be solved.

The following short key should serve for the identification of larvae of mosquitoes most likely to be found in tree holes in the eastern half of the United States. Name in square brackets are of mosquitoes that do not routinely breed in cavities, and hence are not as likely to be encountered as the other species.

KEY TO FOURTH INSTAR MOSQUITO LARVAE MOST LIKELY TO BE FOUND IN TREE HOLES IN THE EASTERN HALF OF THE UNITED STATES

1. Eighth abdominal segment without siphon or air tube 2
   Eighth abdominal segment with a siphon or air tube as long as or longer than wide 3
2. Head hairs 5, 6, and 7 (frontal head hairs) small, not plumose; hair 6 (lateral hair) of abdominal segments 1 to 6 large and plumose ..... **Anopheles barberi** Coq.
   Head hairs 5, 6, and 7 large and plumose; hair 6 of abdominal segments 4 to 6 not plumose ..... [**Anopheles punctipennis** (Say)]
3. Siphon without pecten teeth 4
   Siphon with pecten teeth 6
4. Comb scales of abdominal segment 8 replaced by a large sclerotized plate with two large setae on its posterior edge ..... **Toxorynchites rutilus** (Coq.)[2]
   Comb scales of abdominal segment 8 consisting of two rows, the posterior row being in the form of long pointed rods 5
5. Eighth abdominal segment without a sclerotized plate; head hair 9 (transutural hair) multiple and barbed; larvae light in color ..... **Orthopodomyia alba** Baker
   Eighth abdominal segment (and sometimes seventh and sixth) with a large sclerotized plate; head hair 9 single or branched only distally; larvae dark in color ..... **Orthopodomyia signifera** (Coq.)
6. Siphon with a pair of tufts at base; pecten continued distally by a row of long hairs ..... [**Culiseta inornata** (Williston)]
   Siphon without basal tufts, but with one or more pairs of hairs or tufts more distally; pecten not continued distally by a row of long hairs 7
7. Siphon with several pairs of tufts or single hairs 8
   Siphon with only one pair of tufts 10
8. Antennal hair (hair 1) arising near center of antenna; hairs of siphon mostly single ..... [**Culex restuans** Theo.]
   Antennal hair arising near outer third of antenna; hairs of siphon mostly multiple 9
9. Head hairs 5 and 6 (upper and lower head hairs) with more than three branches; subapical siphonal hair tuft inserted laterally out of line with other tufts ..... [**Culex quinquefasciatus** complex]
   Head hairs 5 and 6 usually single, rarely with two or three branches; apical hair tuft (and sometimes subapical) often inserted out of line with other tufts ..... [**Culex territans** Walker]
10. Siphonal hair tuft inserted within the pecten ..... [**Aedes atropalpus** (Coq.)]
    Siphonal hair tuft inserted beyond pecten 11
11. Head hair 5 (upper head hair) multiple; comb scales arranged in a triangular patch ..... **Aedes thibaulti** D. and K.
    Head hair 5 single (or rarely double); comb scales in a single, sometimes irregular, row 12
12. Head hair 7 (preantennal hair) single; individual comb scale with a large median spine and several short, stout lateral spines ..... [**Aedes aegypti** (Linn.)]
    Head hair 7 with more than one branch; individual comb scale without stout lateral spines, although sometimes evenly fringed with fine spinules 13
13. Ventral brush of eighth segment without preantal tufts; dorsal posterior area of saddle or dorsal plate of ninth segment with large, obvious denticles 14
    Ventral brush with one or more preantal tufts; dorsal posterior area of saddle without denticles or with small, inconspicuous ones 15
14. Head hair 6 (lower head hair) single; lateral hair of ninth segment with two or three branches ..... **Haemagogus equinus** Theo.
    Head hair 6 double; lateral hair of ninth segment with four to six branches ..... **Haemagogus** species
15. Head hair 6 (lower head hair) single; individual scale sharp on end and not fringed distally with small spinules ..... **Aedes muelleri** complex
    Head hair 6 double or multiple; individual comb scale blunt on end and fringed distally with small spinules 16
16. Saddle or dorsal plate of ninth segment with a definite hole or depression near ventral margin; ventral margin of saddle often reaching to or below middle of segment ..... **Aedes zoosophus** D. and K.
    Saddle of ninth segment without a definite hole or depression; ventral margin of saddle often not reaching middle of segment ..... **Aedes triseriatus** (Say)

[2] The larvae of the two so-called subspecies *T. r. rutilus* (Coq.) and *T. r. septentrionalis* (D. and K.) are indistinguishable. *T. r. rutilus* is known at present only from a few localities in the extreme southeastern United States.

REFERENCES CITED

Bohart, Richard M. 1948. The subgenus *Neoculex* in America north of Mexico (Diptera, Culicidae). Ann. Ent. Soc. America 41: 330–45.

Breland, Osmond P. 1949. Distinctive features of the larvae of *Aedes alleni* Turner (Diptera, Culicidae). Jour. New York Ent. Soc. 57: 93–100.

1954. Notes on collecting mosquitoes. Mosquito News 14: 173–75.

1957a. Some factors that might influence the reintroduction of the yellow fever virus into the United States. Texas Jour. Sci. 9: 262–6.

1957b. Some techniques for collecting of tree hole breeding mosquitoes. Mosquito News 17: 305–8.

Eads, R. B., and **L. G. Strom.** 1957. An additional United States record of *Haemagogus equinus*. Mosquito News 17: 86–9.

Elton, N. W. 1956. Yellow fever in Central America, the imminent threat to Mexico and the United States. Amer. Jour. Publ. Health 46: 1259–65.

Hedeen, Robert A. 1953. The biology of the mosquito *Aedes atropalpus* Coquillett. Jour. Kansas Ent. Soc. 26: 1–10.

Jenkins, Dale W., and **Stanley J. Carpenter.** 1946. Ecology of the tree hole breeding mosquitoes of Nearctic North America. Ecol. Monogr. 16: 31–47.

Levi-Castillo, Roberto. 1951. Los mosquitos del genero *Haemagogus*-Williston, 1896 en America del Sur. 77 pages. Cuenca, Ecuador: Editorial "Don Bosco."

Rodaniche, E. de, and **P. Galindo.** 1957. Isolation of yellow fever virus from *Haemagogus mesodentatus*, *H. equinus*, and *Sabethes chloropterus* captured in Guatemala in 1956. Amer. Jour. Trop. Med. Hyg. 6: 232–7.

Soper, Fred L. (chairman). 1955. Yellow fever conference. Amer. Jour. Trop. Med. Hyg. 4: 571–661.

Trapido, Harold, and **Pedro Galindo.** 1956. Genus *Haemagogus* in the United States. Science 123: 634.

THE EXTERNAL ANATOMY OF THE LARVA OF NACERDES MELANURA (LINNAEUS)[1]
(COLEOPTERA: OEDEMERIDAE)

JEROME G. ROZEN, JR.
Entomology Research Division, Agr. Res. Serv., U.S.D.A.

Soon after commencing a taxonomic study of larvae of the Oedemeridae, I discovered that there was no single publication which could be consulted in order to gain an understanding of their anatomy. Consequently I undertook a study of the exoskeleton of the mature larvae of *Nacerdes melanura* (Linnaeus), a common representative of the family. The investigation revealed that the morphological terms that had been applied to beetle larvae were not always consistent with modern practices. More important, however, was the fact that the homologies of some of the structures had been misinterpreted or were unknown. This paper, therefore, is intended to serve two purposes: to establish the homologies of the external structures of the mature larva of *Nacerdes melanura* and to provide a terminology that conforms with present-day usage in insect morphology. I believe, however, that the material may have a broader application. An examination of representatives of a number of coleopterous families reveals that the morphological terms and the concepts of the structures presented here can be applied to most legged orthosomatic beetle larvae. Furthermore, since it seems likely that this type of larva gave rise to the various grub-shaped and apodous forms, the investigation would seem to be a necessary step in interpreting homologies throughout the order.

It has not been possible to determine with certainty the true homologies of some of the parts. While these problems are mentioned in the description, the more important ones are summarized at the end of the paper.

Wherever possible, the terminology of Snodgrass (1935) has been adopted, but otherwise an attempt has been made to employ suitable terms that are already in the literature.

TECHNIQUES

Most of the external anatomy of the larva of *Nacerdes melanura* is interpreted by an examination of cleared specimens. Clearing may be accomplished by making a series of incisions along one side of the body and then gently boiling the specimen in an aqueous solution of potassium hydroxide until the muscle fibers and fat tissue are dissolved. (In treating smaller or more delicate larvae than that of *N. melanura*, it would probably be advisable not to heat the specimens in potassium hydroxide solution, but merely to leave them in the agent at room temperature until cleared.) The tracheae and the contents of the digestive tract must be removed through one of the incisions. The completely cleared specimen should be washed in water containing a few drops of glacial acetic acid and then lightly stained with acid fuchsin. A specimen prepared in this way retains its original shape, and the cuticular thickness is indicated by the intensity of the stain. The larva can be examined and drawn while in glycerine and may be stored in alcohol.

A study of the exoskeleton alone was not always sufficient to determine the correct homologies; it was often necessary to examine the musculature. Although the muscles are not illustrated, they are mentioned in appropriate places in the following description. An interpretation of the homologies of certain structures proved so difficult that it was necessary to pursue collateral studies of larvae of other species. Consequently the cervical region of *Staphylinus* and the thoracic sterna of the oedemerid *Calopus angustus* LeConte are discussed below.

HEAD
(Figs. 1-7, 9, 12, 13, 16)

The cranium (figs. 1, 2) is a large, broad, flattened, somewhat asymmetrical capsule, which, though slightly nutant, is essentially prognathous. The moderately heavily sclerotized integument bears no pigments except for the sclerotized portion of the anteclypeus, which has a somewhat brownish hue, and for traces of brown along the pleurostomal and hypostomal thickenings, especially in the vicinity of the articulations of the mandibles. A very short distance laterad of each mandible and in the same horizontal plane, the anterior portion of the cranium is produced into a low protuberance from which the antenna arises. Just laterad of these prominences is a group of small, indefinite subcuticular dark blotches (not illustrated), which are the sole indications of *ocelli*.

CRANIAL RIDGES, SUTURES, AND APODEMES.—The posterior part of the cranium is margined by the distinct internal postoccipital ridge (figs. 1, 2, *PocR*). This ridge runs in a nearly straight line along the upper surface of the head, but ventrally it extends obliquely forward on each side of the posterior tentorial pits. The ventral arms of this thickening become less pronounced along the sides of the gula, but are indicated externally

[1]Accepted for publication August 1, 1957.

as sutures, the *gular sutures* (fig. 2, *GuS*). The *posterior tentorial pits* (fig. 2, *PTP*) are conspicuous, deep, crescent-shaped inflections. On each side of the head the *hypostomal ridge* is virtually obsolete between the posterior tentorial pit and the point of articulation of the cardo. As a consequence the lateral portions of the postmentum appear continuous with the postgenal areas (fig. 2). From the articulation of the maxilla to the attachment of the hypopharyngeal bracon each ridge is scarcely in evidence, but borders the corium at the base of the maxilla. The hypopharyngeal bracon (discussed below) connects with the ridges immediately posteriad of the ventral articulation of the mandible (fig. 2, *a'*). Each *pleurostomal ridge* (fig. 1, *PR*) is well developed and dark in the vicinity of the articulations of the mandibles, but between the articulations it is relatively weak and but lightly pigmented. The anterior tentorial arms (fig. 1, *AT*) arise from these ridges near the dorsal articulations, but external pits are scarcely if at all noticeable. The epistomal ridge (and corresponding suture) is completely lost, as is more fully explained below. However, there is a pronounced internal transverse thickening (fig. 1, *IclpR*) which connects the pleurostomal ridges across the front of the face. Superficially it appears to be the epistomal ridge and has been so termed in the past. In actuality it is merely a thickening of the clypeus, acting as a brace for the mouth frame, and therefore can be regarded as the dorsal counterpart of the hypopharyngeal bracon. Boving (1954) has applied "epistoma" to it, but since that word connotes the epistomal suture, I believe that "*intraclypeal ridge*" is more suitable (corresponding to the term intraclypeal suture of Cook, 1944).

A shallow *median epicranial sulcus* (fig. 1, *MES*) (and associated internal ridge) extends forward from the posterior margin of the head for about a quarter of the length of the cranium. At its anterior end the sulcus divides, forming two narrowly diverging frontal sulci. Two other sulci (fig. 1, *DES*) and accompanying ridges arise from the posterior margin of the head, one on each side. Each roughly parallels the lateral margin of the head when viewed from above and terminates less than half way to the antenna. Corresponding grooves on the elaterid larva have been called the dorsal epicranial sulci by Hyslop and Boving (1935), and Glen (1950) has adopted this term in his scholarly work dealing with the Lepturoidini of the same family. However, it seems more appropriate to call them *dorsolateral epicranial sulci*, because of their position and because of possible confusion of terminology with respect to the median epicranial sulcus.

The *anterior tentorial arms* (fig. 1, *AT*) appear as short, thin, slightly curved apodemes which arise from the pleurostomal ridge and extend obliquely backward toward the median line. They end freely in the cranial cavity and do not approach the posterior arms. In comparison with the anterior ones, the *posterior tentorial arms* (figs. 13, 16) are well developed and their shape is rather complicated, as depicted. They extend upward in an anterior direction toward the anterior portion of the stomodaeum, near the buccal cavity. They converge apically but do not meet. A thinner *tentorial bridge* (figs. 13, 16, *TB*) joins them near their bases. This structure arches upward medially and thus permits the nerve cords of the central nervous system to pass beneath it.

Aside from the tentorium there are a number of conspicuous apodemes within the head capsule. A pair arise from the essentially membranous suspensorial area of the hypopharynx near the mouth. They extend upward and backward and provide for the insertion of the retractor muscles of the mouth angle. The apodemes of the mandibles and of the cardines are discussed in connection with appendages of the mouth.

Cranial Areas.—The cranium can be divided into a number of different areas, which, however, can not always be precisely delineated. Considering first the ventral surface of the head, the gula (fig. 2, *Gu*) is defined as the region bounded laterally by the gular sutures (ventral arms of the postoccipital suture) and anteriorly by an imaginary transverse line drawn just behind the posterior tentorial pits. Although its anterior portion is distinctly sclerotized and is continuous with the postmentum, the posterior portion appears membranous but can be identified by the insertion of the ventral thoracic muscles which retract the head. The *postocciput* is virtually obsolete with the exception of the gula, which can probably be regarded as a ventral modification of it in the prognathous type of head. On each side of the gula is the *postgena* (fig. 2, *Pge*). The limits of this area have been variously defined with respect to coleopterous larvae. However, Snodgrass (1935) considers its inner boundary to be composed of the hypostomal ridge and a portion of the pleurostomal ridge as well as the gular suture. In *Nacerdes melanura* the position of the outer boundary is open to question since there is no occipital suture. However, the postgena should probably be considered as occupying most of the ventral surface of the head on each side, as indicated by Snodgrass (*ibid.*, fig. 67). Because of the absence of an occipital suture, the postoccipital ridge demarcates the posterior margins of the *parietals* (fig. 1, *Ptl*). Each parietal extends from the indefinite outer boundaries of the postgena to the median epicranial sulcus and to the imaginary line extending between the anterior terminus of the frontal sulcus and the dorsal mandibular articulation (fig. 1, *c*) (dorsal end of the pleurostomal ridge).

The *frontoclypeal area* (fig. 1, *Pclp, Fr*) lies between the frontal sulci and their imaginary

extensions. Its posterior portion (frons) is defined not only by these sulci, but also by the origins of the posterior labral muscles and the retractor muscles of the mouth angles, both sets lying behind the frontal ganglion connectives. The anterior (postclypeal) portion is indistinguishably united with the frons and lies behind the intraclypeal sulcus. It bears the origin of the dilator muscles of the cibarium and of the dorsal muscles of the buccal cavity, all of which are situated anterior to the frontal ganglion connectives. Because of the origin and position of these various muscles, it is obvious that the intraclypeal sulcus can not be regarded as the epistomal suture. The area in front of the sulcus is the *anteclypeus* (fig. 1, *Aclp*) and possesses a posterior, somewhat asymmetrical sclerotized portion and an anterior membranous region which permits the retraction of the labrum. Ventrally the epipharyngeal surface of the cylpeus forms the dorsal wall of the cibarium and is membranous (excluding the tormae which are presumably derived from the labrum) except for two lateral sclerites, here called the *dorsal cibarial sclerites* (fig. 5, *DCB*). These structures lie below the anteclypeus, and each connects to the sclerotized posterior portion of the labral epipharynx by a long, narrow, sclerotized band.

The *labrum* (fig. 1, 5, *Lm*) is a flattened asymmetrical lobe which bears an irregular sclerotized band ventrally along its posterior margin. The two long, proximately situated *tormae* (fig. 5, *Tor*) arise from this sclerotization and extend back onto the epipharyngeal surface of the clypeus. At their extremities they fuse, forming there a single internal projection to which attach the paired posterior labral muscles. The labral epipharynx is slightly produced ventrally along the median line and possesses a dense mat of short fine hairs in the region of the tormae. This brush opposes a similar one located on the prehypopharynx. The proximal part of the *hypopharynx* (fig. 12) is membranous and forms the floor of the cibarium, while the membranous suspensorial area composes the sides and connects the mouth to the base of the mandible. The distal part of the hypopharynx consists of a median, heavily sclerotized, darkly pigmented, adorally flattened lobe, the hypopharyngeal sclerome (fig. 12, *HphyScl*), which projects anterodorsally toward the epipharyngeal surface. At the base the lobe connects to, or more probably forms, the middle section of the *hypopharyngeal bracon* (fig. 12, *HB*).

The hypopharyngeal bracon is a rodlike brace which stretches across the ventral surface of the head (fig. 2). While the middle section of the rod is internal, lying above the labrum, the lateral portions are situated in the ventral membrane between the bases of the maxillae and mandibles. Each of the lateral sections divides into a thicker ventral continuation of the middle section and a thinner somewhat anterodorsally directed arm. The former fuses with the hypostomal ridge just behind the ventral articulations of the mandible (fig. 2, *a'*), while the arm attaches to the base of the mandible just above the ventral condyle, on the axis of rotation of the mandible. The hypopharyngeal bracon and the intraclypeal ridge serve together as an immovable frame to provide a firm base for the mandibular articulations. An apically pilose, elevated projection (fig. 12, *Prhphy*) arises immediately anterior to the median hypopharyngeal sclerome. Similarly situated, though more extensive, hairy surfaces in other beetle larvae have been called *prehypopharynges* (St. George, 1929). Although this is a good descriptive term, the derivation of the structure is unknown and the prehypopharynx may actually represent a modification of the dorsal surface of the labium rather than a differentiation of the hypopharynx.

Appendages of the Head.—The *antennae* (fig. 9) are moderately long, three-segmented appendages. Each segment is smaller in diameter than the preceding, and the second bears apically a small conical "sensory" appendix (fig. 9, *SApdx*), which lies below the third segment.

The darkly pigmented, massive *mandibles* (figs. 3, 4, 6, 7) are of the molar type. Each is composed of an apical, distally tapering portion, the inner surface of which is concave, and a more or less quadrate basal portion, the inner surface of which forms the mola. The molar surface consists of a series of transversely directed (with respect to the long axis of the mandible), parallel, evenly spaced, small ridges (approximately 20 on the left mandible but many more on the right). Aside from these features, the right and left mandibles are markedly different from each other; the dissimilarities pertain primarily to the teeth and to the contour of the molar area. On the left mandible (figs. 3, 4) there are three large apical teeth, the middle one being the longest. In addition, there are two smaller teeth on the dorsal inner edge which are subapical in position. When viewed from above (fig. 3) or below, the distal end of the molar surface forms a sharp right angle with the basal portion of the apical concavity. The molar surface itself appears rather flat, although apically it curves perceptibly outward along the dorsal surface of the mandible, where it is margined by a small, elongate pitlike concavity (figs. 3, 4, *p*). Near the base of the molar surface there is a shallow depression (figs. 3, 4, *d*) in which the transverse ridges become obliterated, although a ridgelike basal margin of the molar surface may be evident. The area between the base of the mola and the base of the mandible is in the same plane as the molar surface. The very large abductor apodeme of the mandible arises at the base of the inner surface and the smaller abductor apodeme, at the base of the outer. The right mandible, like the left, also

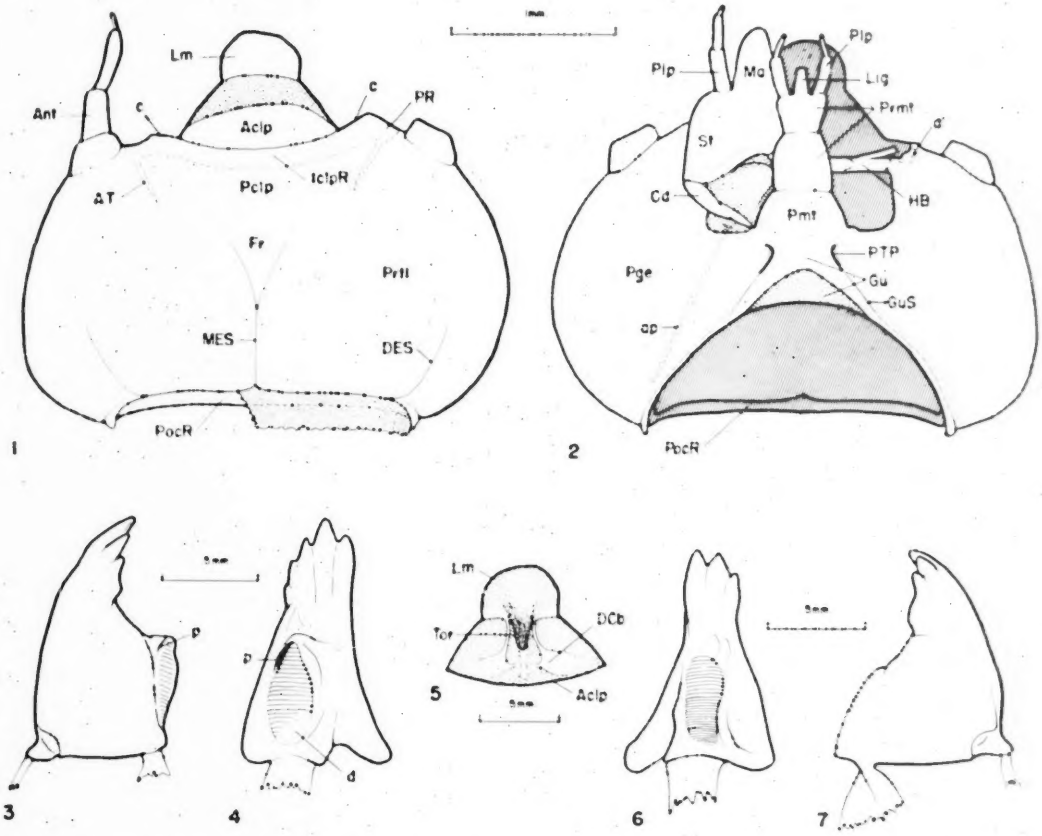


Fig. 1, head, dorsal view (mandibles and maxillae removed); fig. 2, same, ventral view (mandibles and left maxilla removed); fig. 3, left mandible, dorsal view; fig. 4, same, inner view; fig. 5, epipharyngeal surface of labrum and anteclypeus; fig. 6, right mandible, inner view; fig. 7, same, dorsal view.

EXPLANATION OF ABBREVIATIONS

a', ventral mandibular articulation
Ac, antecosta
Aclp, anteclypeus
Amp, ampulla
An, anus
Ant, antenna
ap, dorsal abductor apodeme of cardo
AT, anterior tentorial arm
Bs, basisternum
c, dorsal mandibular articulation
Cd, cardo
Cx, coxa
d, depression
DCb, dorsal cibarial sclerite
DES, dorsolateral epicranial suleus
Epm, epimeron
Eps, episternum
Fm, femur
Fr, frons
Gu, gula
GuS, gular suture
H, head
HB, hypopharngeal bracon
HphvScl, hypopharyngeal sclerome
IclpR, intraclypeal ridge
Ipl, intersegmental pleurite
J, jugulare
k, sternocostal suture
Lig, ligula
Lm, labrum
Mx, mala
MES, median epicranial suleus
p, pitlike concavity
pclp, postclypeus
Pcx, postcoxale
Pge, postgena
Plp, palpus
PlS, pleural suture
Pmt, postmentum
PocR, postoccipital ridge
PR, pleurostomal ridge
Prcx, precoxale
Phphy, prehypopharynx
Prmt, prementum
Ptar, pretarsus
Prtl, parietal
PT, posterior tentorial arm
PTP, posterior tentorial pit
r, ridge
S, sternum
SA, sternal apophysis
SApdx, "sensory" appendix
Sl, sternellum
Sp, spiracle
Spn, spina
Ss, spinasternum
St, stipes
T, tergum
TB, tentorial bridge
Tbtar, tibiotarsus
Tor, torma
Tr, trochanter

possesses three large teeth, but here the ventral one is the longest and the dorsal one the shortest. There are no distinct small subapical teeth along the dorsal inner edge. The molar area is much more produced at the base than on the left mandible, so that, when the inner edge is viewed from above (fig. 7) or below, the proximal portion of the apical concavity forms a continous curve with the molar surface, and the inner base of the mandible lies considerably laterad of the base of the mola.

The other paired appendages of the head are symmetrical, very lightly pigmented, and when viewed from below (fig. 2) arise posterior to both the hypopharyngeal bracon and the bases of the mandibles. Each *maxilla* possesses a narrow cardo (fig. 2, *Cd*) which widens somewhat apically. When viewed from below the cardo bears near the base a constriction or narrowing which is associated with an internal ridge. Because of this modification in this and other oedemerids, the cardo has often been regarded as being two segmented or "divided". However, it is clearly a single sclerite both in this species and in all the others which were available for study. The very long, thin dorsal abductor apodeme (fig. 2, *ap*) of the cardo attaches to the corium a short distance from the constriction. Its point of attachment to the corium is marked by a pit, and the corium between the pit and the constriction is thickened and microscopically striated. The apodeme stretches toward the posterolateral wall of the cranium upon which the associated muscles take their origin. Although the corium is small laterad of the cardo, that portion which lies between the cardo and the postmentum is extensive and has a number of conspicuous folds. It has often been called the maxillary articulating membrane. The stipes (fig. 2, *St*) is indistinguishably united with the mala (fig. 2, *Ma*), which itself represents the fused galea and lacinia. These combined parts form a flattened, hatchet-like structure. Along the curved inner edge of the mala are many erect, darkly pigmented, stout hairs and a single short, nonmovable spine (hidden behind the labial palpus, in fig. 2). The palpus, which is composed of three cylindrical segments, arises adjacent to the mala at the distal end of the stipes. The labium (figs. 2, 12) is divided into a distal, anteriorly directed, conical ligula (*Lig*), a first prementum (*Prmt I*), a second prementum (*Prmt II*), and a postementum (*Pmt*), which fuses with the gula. Although these divisions have been commonly called the ligula, prementum, mentum, and submentum, respectively, the origin and insertion of the retractor muscles of the prementum clearly establish the true homologies, as Anderson (1936) has demonstrated in other coleopterous groups. A two-segmented palpus (*Plp*) arises from each of the anterolateral angles of the first prementum.

THORAX
(Figs. 8, 10, 14, 15)

The thorax tapers slightly posteriorly, appears totally unpigmented except for the coxal articulations and the dorsal asperities, and is generally very weakly sclerotized. Because of this last feature, it is not always possible to delineate the boundaries of the sclerites and, in some instances, to determine whether or not they are present.

A rather long membranous *cervix* attaches the head to the thorax and permits the head to be partly withdrawn into the prothorax. Ventrally it contains a large though weak and inconspicuous sclerite (figs. 8, 14, *J*), which in *Nacerdes melanura* fuses posteriorly with the basisternum of the prothorax. This sclerite has often been called the "presternum" of the prothorax. However, a study of the musculature of the well-developed "presternum" of *Staphylinus* reveals that most (but not all) of the muscles correspond to those associated with the jugular sclerite, or jugulare, of the megalopteran *Corydalus* (Kelsey, 1954). Consequently, musculature plus position suggest that the "presternum" of the prothorax of Coleoptera larvae represents a fusion of the cervical sclerites and "other undetermined intersegmental sclerites" (*ibid.*).

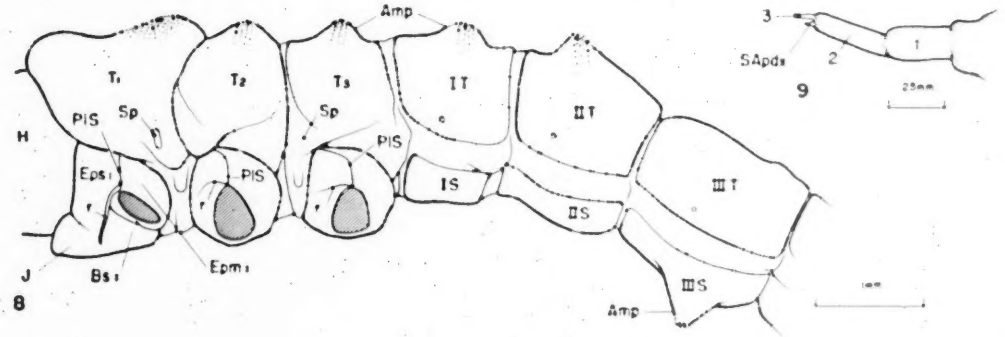
Dorsum.—Each of the thoracic terga bears paired patches of posteriorly directed, crescent-shaped asperities.

The convex pronotum (fig. 8, T_1) represents the longest of the thoracic terga. Anteriorly its sclerotization weakens, so that the anterior boundary is difficult to detect. In a similar fashion the lateral margin of this tergum and also of the following two are indefinite, the terga appearing to intergrade with the lateral membrane. The posterior portion of the pronotum is incised by a deep longitudinal median groove. The *mesonotum* (figs. 8, 10, T_2) and *metanotum* (fig. 8, T_3) are distinctly shorter than the pronotum, and each is produced into paired sublateral convexities, termed ampullae (fig. 8, *Amp*), upon which are situated the asperities. The antecosta (fig. 10, *Ac*) appears as a weak subapical internal ridge on each of these two segments.

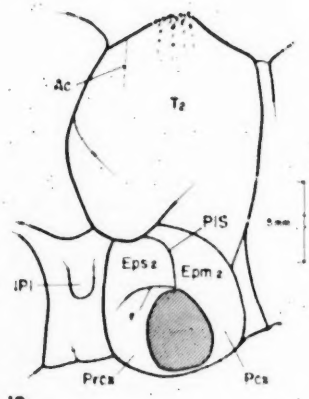
The anterior pair of *thoracic spiracles* (fig. 8, *Sp*) are elongate-oval and large, exceeding in size those of the abdomen. Each is situated in the lateral membrane above and a little anterior to

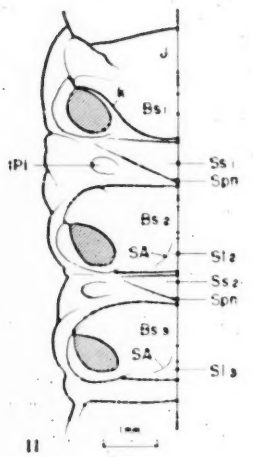
EXPLANATION OF FIGURES

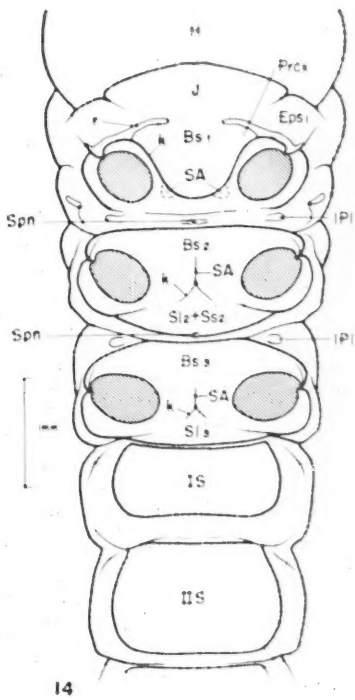
Figs. 8–10, 12–17. *Nacerdes melanura* (Linnaeus); fig. 11, *Calopus angustus* LeConte. Fig. 8, thorax and anterior part of abdomen, lateral view; fig. 9, antenna, lateral view; fig. 10, mesothorax, lateral view; fig. 11, right half of thorax, ventral view; fig. 12, labium and hypopharynx, lateral view; fig. 13, posterior tentorium, lateral view; fig. 14, thorax and anterior part of abdomen, ventral view; fig. 15, left leg, anterior view; fig. 16, posterior tentorium, posterior view; fig. 17, posterior part of abdomen, lateral view.

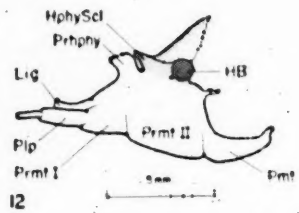

Amp
T1
T2
T3
IT
IIT
H
PIS
Sp
Eps1
PIS
Sp
PIS
IS
IIIT
IIS
J
Bs1
Epm1
IIIS
Amp
8

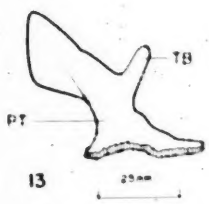
3
SApds
2
1
9

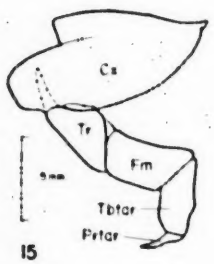

Ac
T2
PIS
Eps2
Epm2
IPl
Prcx
Pcx
10

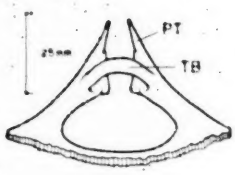

J
Bs1
IPl
Ss1
Spn
Bs2
SA
St2
Ss2
Spn
Bs3
SA
St3
11

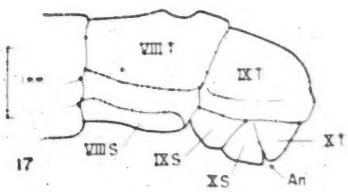

H
Prcx
J
Eps1
Bs1
SA
Spn
IPl
Bs2
SA
St2+Ss2
Spn
IPl
Bs3
SA
St3
IS
IIS
14


HphyScl
Prhphy
Lrg
HB
Plp
Prmt II
Prmt I
Pmt
12


TB
PT
13


Cx
Tr
Fm
Tbtar
Prtar
15


PT
TB
16


VIII T
IX T
X T
VIII S
IX S
X S
An
17

the intersegmental pleurite. Their position therefore appears to be prothoracic. The other pair of thoracic spiracles are vestigial, presumably nonfunctional, and located on the anterior portion of the metathorax.

PLEURAL REGION.—The pleural suture (fig. 8, *Pls*) of the propleuron is conspicuous and the corresponding internal ridge strongly developed, being produced into an internal apophysis. A thick internal ridge (fig. 8, *r*) (and accompanying suture), which corresponds to the ridge *r* (figs. 8, 10) on the meso- and metathorax, branches from the pleural ridge a short distance from the coxal cavity and from there extends more or less transversely (as seen in ventral view, fig. 14) a short distance across the basisternum. The precoxale can probably be defined as that small sclerotized area which lies between the ridge *r* and the coxal cavity. It widens below, where it fuses with the basisternum. The area anterior to the pleural suture and the ridge *r* represents the episternum (fig. 8, Eps_1), the lower margin of which abuts the jugulare. Posterior to the pleural suture is the nearly membranous epimeron (fig. 8, Epm_1), below which is the apparently membranous postcoxale. In the membrane which separates the epimeron of the prothorax from the episternum of the mesothorax there is a small, convex semimembranous plate, the intersegmental pleurite (fig. 10, *IPl*). A similar sclerite is situated on each side between the meso- and metathorax. The *mesopleuron* and *metapleuron* are virtually identical in appearance. Each possesses a pleural suture (fig. 8, 10 *Pls*) which arises from the coxal articulation and then curves forward. Another pronounced internal ridge (and external suture) (figs. 8, 10, *r*) extends in an anteroventral direction from the coxal articulation but tends to become weaker anteriorly. On the basis of position this ridge would seem to provide a suitable boundary separating the episternum (fig. 10, Eps_2) from the precoxale (*Prcx*) below. The precoxale appears to be united with the sternum. Posterior to the pleural suture and the coxal cavity are found the nearly membranous epimeron (fig. 10, Epm_2) and the actually or apparently membranous postcoxale (*Pcx*).

VENTER.—The basisternum (fig. 14, Bs_1) of the prosternum is a large, relatively heavily sclerotized, convex sclerite, the anterior portion of which fuses with the jugulare (*J*). Its posterior margin is well marked by the sternocostal suture (*k*). The lateral portions of this suture lie in front of the coxal cavities but then curve posteriorly so that the median section of the suture aligns with the hind margins of the coxae. Internally the sternocostal ridge is well developed and gives rise to two sublateral apophyses, the sternal apophyses (*SA*). The basisternum, like the pronotum, provides attachment for some of the strong longitudinal muscles that move the head, and thus can easily be distinguished from the enlarged jugulare of such groups as the Pyrochroidae.

The remaining portion of the venter of the thorax is difficult to interpret because of lack of sclerotization. Although the area between the basisternum of the prothorax and that of the mesothorax may have become entirely membranous, an examination of the larva of the oedemerid *Calopus angustus* (see fig. 11) suggests that the sternellum has been displaced by the enlarged prothoracic basisternum. A membranous area mesad of each coxal cavity may represent a remnant of it. At any rate, the intersternite (spinasternum) of *Nacerdes melanura* is membranous, but the median pitlike spina (fig. 14, *Spn*) is evident just in front of the following basisternum.

The sternal plates of the mesothorax and the metathorax are weakly sclerotized but each possesses an inverted Y-shaped median thickening. The arms (fig. 14, *k*) provide attachment for some of the longitudinal sternal muscles and may therefore be termed the sternocostal ridge. Other longitudinal muscles originate on or somewhat posteriad of imaginary extensions of the arms. The longitudinally directed median part (fig. 14, *SA*) of this thickening is strongly produced internally and almost certainly represents the combined sternal apophyses, for the rotator muscles of the coxae take their origin thereon. (These apophyses are somewhat separated in *Calopus angustus*, fig. 11.) The sternellum (fig. 14, *Sl*) lies immediately behind the sternocostal ridge, and laterally its anterior margin fuses with the basisternum. In the mesothorax the sternellum (Sl_2) and intersternite (Ss_2) are united, and the median pitlike spina (*Spn*) is situated on the posterior margin of the plate. The intersternite between the metathorax and abdomen is presumably lost. In *Calopus angustus* (fig. 11) the intersternite (Ss_3) between the meso- and metathorax remains as a distinct semimembranous area, separated from the eusternum of the mesothorax by a membrane.

The *legs* (fig. 15) are moderately short but well developed and similar to one another in appearance. Those of the same body segment are widely separated at the base. The coxa (*Cx*) is mesally directed, and its inner apical surface is produced into a projecting lobe. The trochanter (*Tr*), femur (*Fm*), and tibiotarsus (*Tbtar*) are more or less cylindrical, subequal in length, and followed by the moderately long, tapering pretarsus (*Prtar*), which is darkly pigmented apically. That this last segment does not represent a combined pretarsus and tarsus is indicated by its lack of a levator muscle.

ABDOMEN

(Figs. 8, 14, 17)

The abdomen is very weakly sclerotized and completely unpigmented except for the asperities.

In most preserved specimens it appears to bend downward between the first and second segments (fig. 8). Because the tergum of the ninth segment curves posteriorly while the sternum is shortened, the tenth segment is ventral (fig. 17).

DORSUM.—The tergum of each segment is apparently represented by a single large plate which extends laterally to include the spiracles. The tergum (fig. 8, *I T*) of the first segment is produced into two sublateral asperity-bearing convexities, called ampullae (fig. 8, *Amp*), so that it resembles the metatergum. An antecostal suture is not evident, and the antecosta is indistinct but lies at the anterior base of the convexities and can be distinguished in cleared specimens because the posterior portion of the tergum is thicker than the acrotergite. The second abdominal tergum (*II T*) is similar to the preceding except there is but a single large median convexity, the asperities of which are directed dorsally rather than somewhat posteriorly. The terga of segments three to eight are similar to each other. All are simple plates with either weak or apparently absent subapical antecostae. However, the position of the antecostal ridges can be detected by the insertion of the longitudinal muscles arising from the preceding segment. The posterior portion of the ninth tergum (fig. 17, *IX T*) curves downward, so that the surface of the small tenth tergum (*X T*) is at approximately right angles to the long axis of the body.

The spiracles are located on the lateral portion of the terga and are an oval type, possessing a series of air tubes along the posterior lip. The first spiracle is usually slightly larger than the others, which are subequal in size.

PLEURAL REGION.—At first glance the pleural region appears to be the membranous strip (figs. 8, 17) extending along the sides of the abdomen. An examination of *Oedemera virescens* (L.) and *Pytho americanus* Kby., both of which bear sclerites in this membranous area, suggests that the membrane is derived mostly from the dorsum. The true dorso-pleural line seems to be near or at the ventral boundary of this membrane. If so, the pleural region of each abdominal segment either is very narrow or has become sclerotized and incorporated with the sternal plate.

VENTER.—The sterna (*S*) of abdominal segments one, two, and five through eight are similar in that each is a single large plate. The first sternum is shortest. The third and fourth differ from the others by each possessing two large conical sublateral protuberances, termed ampullae (fig. 8, *Amp*), which are apparently movable and probably function as prolegs. Each ampulla bears a patch of ventrally directed asperities which cover the apex and the apical portion of the inner side. The ninth sternum is relatively short, and the tenth, even more reduced and but indistinctly sclerotized. None of the sterna bear an antecosta; the longitudinal muscles from the preceding segment are attached to the anterior margin of the plate (except in the case of the first sternum).

In ventral view there is a transverse slit bordered anteriorly by the tenth abdominal sternum and posteriorly by the corresponding tergum. However, the tergum and sternum are capable of being separated to reveal the true anal opening (fig. 17, *An*) surrounded by a somewhat folded, cushion-like membrane which is probably somewhat eversible.

UNSOLVED PROBLEMS

As indicated in the above description, there still exist a number of problems in the understanding of the anatomy of *Nacerdes melanura*, and their solution is necessary for a complete understanding of the morphology of coleopterous larvae in general.

1. In the head the structures around the cibarium deserve further study. Specifically, the origin of the hypopharyngeal bracon is not clear; the fate of the suspensorial sclerites must be regarded as uncertain; and the derivation of the prehypopharynx remains unknown.

2. Although it seems almost certain that the "presternum" of the prothorax is in actuality a cervical sclerite, termed the jugulare, this homology should be confirmed with respect to other coleopterous larvae.

3. The ventral thoracic sclerites seem to be properly homologized. However, because they are poorly sclerotized and hence difficult to delimit, there is a need for further verification.

REFERENCES CITED

Anderson, W. H. 1936. A comparative study of the labium of coleopterous larvae. Smithsonian Misc. Coll. 95(13): 1–29, 8 pls.

Böving, Adam G. 1954. Mature larvae of the beetle-family Anobiidae. Danske Biol. Meddel. 22(2): 1–299, 50 pls.

Cook, Edwin F. 1944. The morphology and musculature of the labrum and clypeus of insects. Microentomology 9(1): 1–35, 18 figs.

Glen, Robert. 1950. Larvae of the elaterid beetles of the tribe Lepturoidini (Coleoptera: Elateridae). Smithsonian Misc. Coll. 111(11): 1–246, 40 figs.

Hyslop, J. A., and **A. G. Böving.** 1935. Larva of *Tetrigus fleutiauxi* Van Zwaluwenburg. Proc. Hawaiian Ent. Soc. 9(1): 49–61, 9 figs.

Kelsey, L. P. 1954. The skeleto-motor mechanism of the dobson fly, *Corydalus cornutus*. Part. I. Head and prothorax. Mem. 334, Cornell Univ. Agric. Expt. Sta. 51 pages, 70 figs.

St. George, R. A. *in* R. T. Cotton. 1929. The meal worms. U. S. Dept. Agric. Tech. Bull. 95: 1–38, 8 figs.

Snodgrass, R. E. 1935. Principles of insect morphology. ix + 667 pages, 319 figs. New York: McGraw-Hill Book Co.

A REVIEW OF THE GENUS SCLERORACUS IN NORTH AMERICA (HOMOPTERA:CICADELLIDAE)

J. T. MEDLER[1]

ABSTRACT

Twenty-eight species and one variety are treated as valid in the genus, all having been described previously. In addition to its inclusion in a key, each species is characterized by a synoptic description and a drawing of the internal male genitalia, and distribution and known host plant records are included. New synonymy: *Scleroracus bullatus* (Ball) (= *Frigartus obesus* Knull) and *S. shastus* (Ball) (= *Euscelis gentilis* Van Duzee).

The genus *Scleroracus* Van Duzee includes species in Europe and North America which are recognized in general by a distinctive pattern of transverse wavy lines on the crown. Oman (1947, 1949) characterized the genus and listed the nearctic species. A number of revisions (Osborn and Ball 1902a, Ball 1928c, and Sleesman 1929a[2]) made valuable contributions towards a knowledge of the genus. However, there has been a need to bring the taxonomy of the species up-to-date and to show certain relationships between the internal male genitalia which were not previously known.

This review was made possible through the assistance of many institutions and workers who generously loaned collections for study, especially the United States National Museum and Kansas University. I undertook this study at the suggestion of Dr. P. W. Oman, and I wish to express my sincere appreciation to him for his kind advice and encouragement.

The host plant relationships of most species in this genus are unknown, and some of the records based only on label data need confirmation. However, it is well established that three plant families, the Caprifoliaceae, Ericaceae and Myricaceae, provide host plants for several species of the genus.

KEY TO SPECIES

1. Species *Limotettix*-like; color lemon-yellow or smoky-yellow; forewing extremely long and narrow, cells but little infuscated 2
   Species some shade of tan, brown or black; forewing not extremely long and tapering, cells usually heavily infuscated, the veins white and prominent . . 3
2. Species 3.5—4.0 mm.; forewing smoky, the commissure darkened rather broadly . . . . . **angustatus**
   Species 4.5—5.0 mm.; forewing light, the commissure darkened very narrowly . . . . . **paludosus**
3. Species shining black; pronotum black; forewing with veins entirely black . . . . . **anthracina**
   Species usually some shade of brown; pronotum with spots; forewing with veins more or less white and contrasting with infuscated cells 4
4. Large Western species (female 5 mm.); crown pale-yellow, a large black spot occupying entire space between ocellus and eye, basal angles of scutellum black . . . . . **bullatus**
   Species not as described 5
5. Species robust (female 5 mm.); forewing with broad contrasting spot at first cross vein, which vein is usually yellow . . . . . **varus**
   Species without a distinctive yellowed spot on the first cross-vein 6
6. Fore and middle femora shining black or very dark brown to just before apex, then abruptly yellow or orange concolorous with tibiae 7
   Fore and middle femora not as described, usually twice banded with fuscous 9
7. Species elongate, pale olive or light brown; forewing of female longer than body . . . . . **osborni**
   Species robust, black or dark brown; forewing of female very little longer than body 8
8. Apical process of aedeagus short and broad in posterior view, tips bifurcate . . . . . **kryptus**
   Apical process of aedeagus long and slender in posterior view, tips acute . . . . . **uhleri**
9. Species 3.5—4 mm.; crown acutely pointed; forewing but little exceeding the body, apical cells broad and relatively short 10
   Species longer than 4 mm.; crown usually obtusely pointed or broadly rounded; forewing definitely longer than body 11
10. Straw-colored; crown without markings or only faintly inscribed . . . . . **humidus**
    Dark brown; crown distinctly inscribed with dark transverse lines . . . . . **arctostaphylus**
11. Transverse lines on crown merged into a very broad red-brown or black band between the eyes; forewing broad, only slightly exceeding the abdomen . . . . . **melastigmus**
    Transverse posterior lines on crown distinctly separated from anterior band, or indistinct 12
12. Species black or very dark brown; crown acutely pointed and with heavy black markings; scutellum largely black, forewing long and narrow 13
    Species usually appearing to be some shade of brown, light brown or ochreous 14
13. Northeastern species; very slender in appearance, crown acutely angled . . . . . **corniculus**
    Rocky Mountain species; rather robust, crown obtusely angled . . . . . **plutonius**
14. Species straw-colored; crown with markings reduced to spots and lines next the eyes; crown broadly rounded and face tumid in lateral view . . . . . **glomerosus**
    Species without a strongly inflated face and broadly rounded crown 15
15. Large Western species (female 5.5 mm.); golden brown; crown obtusely angled, the posterior line wanting, the median line usually reduced to ocellocular spot, but sometimes connected . . . . . **finitimus**
    Species not as described 16
16. Species tawny, large (female 5 mm.); cells of forewing quite uniformly infuscated with light brown. Ocelli red, transverse lines on crown often faded to orange-brown 17

[1]Associate Professor in Agronomy and Entomology, University of Wisconsin, Madison, Wisconsin.

[2]See Metcalf, 1942, for complete reference to literature citations prior to 1942.

Accepted for publication October 10, 1957.

Species usually a darker shade of brown; cells of forewing distinctly margined with fuscous . . . 18
17. Forewing with first cross vein and apices of claval veins at commissure broadly white . . . **omani**
Forewing with cells uniformly infuscated, the veins at commissure not in sharp contrast . . . **symphoricarpae**
18. Large species (female 5.0 mm.); distribution western . . . 19
Smaller species, distribution western and eastern . . . 21
19. Species dark; crown obtusely angled . . . **taramus**
Species with crown acutely angled . . . 20
20. Straw-colored; crown and pronotum faintly inscribed with brown; forewing with supernumary veins on clavus . . . **shastus**
Dark-brown; crown and pronotum heavily marked with black; forewing with cells heavily infuscated **beameri**
21. Species large (female 4.5 mm.); crown tawny with distinctive red-brown inscribed lines, fore and middle femora with a single sub-apical band. Eastern **comptoniana**
Species usually about 4 mm. (female); crown usually inscribed with dark wavy lines; forewings usually infuscated. Species complex identified on basis of the internal male genitalia . . . 22
22. Eastern species . . . 23
Western species . . . 24
23. Crown with dark lines; forewings darkly infuscated, the veins distinct . . . **vaccinii**
Crown unmarked, forewing without infuscations **luteolus**
24. Apical process of aedeagus short and broad in posterior view . . . **dasidus**
Apical process of aedeagus long and slender . . . 25
25. Apical process of aedeagus with distinct spine at shoulder . . . **balli**
Apical process of aedeagus without spine . . . 26
26. Species dark; apical process of aedeagus of same width from base to apex, tips divergent . . . **cacheolus**
Species light brown or tawny; apical process widest at middle, the tips not strongly divergent . . . **myralis**

S. anthracinus (Van Duzee) (Type of the genus)

Scleroracus anthracinus Uhler (nom.nud.).
Conogonus gagates Osborn, 1892, Proc. Iowa Acad. Sci. 1: 126 (nom.nud.).
Athysanus anthracinus Van Duzee, 1894, Can. Ent. 26: 136.
Ophiola anthracina Sleesman, 1929, Ent. Amer. 10: 110.
Scleroracus anthracinus Oman, 1947, Iowa St. Coll. J. Sci. 21: 204.

A distinctive species: shining black, some specimens with trace of yellow on front, and on crown at hind margin. Legs black, the anterior and middle pairs yellow from just before the apex of femora. Length: ♀ 4.2 mm., ♂ 3.9 mm.

Genitalia: Figure 19. Specimen from Elk City, Kas., June 2, 1936, Beamer and Sanderson (KUM). I did not find the aedeagus with apical processes crossed, as illustrated by Sleesman (1929, pl. IX).

Type: ♂ Iowa, Ac. Cat. 370, Gillette (ISCM).

Distribution: One hundred twenty specimens examined from the northeastern and north central United States, but none from Canada. Southern records—South Carolina; Alabama (Garden City); Tennessee (Clarksville); Mississippi (Iuka); Texas (Jefferson); New Mexico (Clouderoft); Arizona (Oak Creek Canyon, 6000 ft.); Western records—Missouri (Oregon Co.); Kansas (Chautauqua Co.); Iowa (Sioux City); Wisconsin (Gays Mills).

Van Duzee (1894, p. 136) stated that he had an example from Colorado from Gillette. Apparently, the Gillette specimen has been preserved: see Oman (1947, p. 204). However, I did not find a single specimen of *anthracinus* among hundreds of leafhoppers examined from Colorado localities; and the most northern record in New Mexico was Tucumcari.

Host Plant: No accurate information is available: labels show mixed vegetation (Iowa) and goldenrod (Long Island). According to Osborn (1915, 1928) it has been taken in small numbers in woods pasture, on hillside pasture, and in grass, in Maine and Ohio.

S. omani Medler

Scleroracus omani Medler, 1955, Ent. News 66: 215.

Species testaceous-orange in general appearance, the markings dark brown; forewing with veins white, a distinct white spot at the apex of each claval vein, on the nervure between claval suture and adjacent claval vein, and on the first cross nervure. Length: female 5.2 mm., male 4.3 mm.

Genitalia: Figure 20, drawn from the type.

Type: ♂, Park Rapids, Minnesota, July 24, 1935, P. W. Oman (USNM).

Distribution: About 30 specimens have been examined from Minnesota, Wisconsin, and Alberta, Canada.

Host Plant: Unknown.

S. kryptus Medler

Scleroracus kryptus Medler, 1955, Ent. News 66: 213.

A robust, darkly marked species, which is indistinguishable from *uhleri* except by an examination of the internal male genitalia. Length: ♀, 4.6 mm., ♂, 4.3 mm.

Genitalia: Figure 21; drawn from the type.

Type: ♂, Muskego, Wisc., July 21, 1939, P. B. Lawson (KUM).

Distribution: Wisconsin, Iowa, Illinois, and Canada (Manitoba, Ontario, and Quebec).

Host Plant: Unknown.

S. uhleri (Ball)

Athysanus (Conosanus) plutonius Osborn and Ball, 1902, Ohio Nat. 2: 240 (not Uhler).
Athysanus (Conosanus) Uhleri Ball, 1911, Can. Ent. 43: 200.
Ophiola uhleri Sleesman, 1929, Ent. Amer. 10: 109.

This black appearing species somewhat resembles *anthracinus*, but usually has yellow markings on front, crown and scutullum. The yellow may be wanting in very dark specimens except for a basal line on the crown. Length: ♀ 4.7 mm., ♂ 4.2 mm.

Genitalia: Figure 5; specimen from Conewago, Pa., 7–1–17, J. G. Sanders (USNM).

Type: ♀, Ames, Iowa, June 29, 1896, E. D. Ball (USNM).

Distribution: One hundred specimens examined from the northeastern and north central

United States, predominantly those States and the Provinces of Canada adjacent to the Great Lakes. The southernmost record in the east was Washington, D. C., and no records were obtained south of Pennsylvania, Ohio, and Kansas. The western limits appear to be North Dakota (Tokio) and Manitoba (Keld, Deepdale). I did not find a single specimen of *uhleri* in collections from Colorado localities.

Host Plant: Not known. According to labels, one specimen, Basking Ridge, N. J., on elm; 2 specimens, Ramsey Co., Minn., in oak forest. According to Sleesman "It has been swept from low ground meadows (Osborn)."

S. uhleri var. speculatus (Ball)

Ophiola uhleri var. *speculata* Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 187.

I could not distinguish this uniformly yellowish brown form with much reduced markings from typical *uhleri*, on the basis of the internal male genitalia.

Type: ♀, Speculator, N. Y., Aug. 6, 1912 (USNM).

Distribution: Nothing can be added to previous records in New York and Pennsylvania.

Host Plant: According to Sleesman (1929, p. 110) "Dr. DeLong reports sweeping it from a sweet fern association".

S. symphoricarpae (Ball)

Athysanus symphoricarpae Ball, 1901, Canad. Ent. 33: 5.
Ophiola symphoricarpae Sleesman, 1929, Ent. Amer. 10: 117.

A light colored, rather robust species; crown tawny, the transverse bands reddish in color. Ocelli red. Length: ♀, 5.0 mm., ♂, 4.5 mm.

Genitalia: Figure 10; specimen from Soldier, Utah, Aug. 13, 1906 (USNM).

Type: ♀, Ridgeway, Colo., July 31, 1900 (USNM).

Distribution: A rather rare species; about a dozen specimens examined from Idaho (Elba); Utah (Soldier Summit); Colorado (Peyton, Ridgway); North Dakota, (Omemee, Knob), and Manitoba (Hartney).

Host Plant: *Symphoricarpos racemosus*.

S. finitimus (Van Duzee)

Euscelis finitimus Van Duzee, 1925, Proc. Calif. Acad. Sci. 14: 422.
Ophiola gentilis Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 187 (not Van Duzee).
Ophiola gentilis Sleesman, 1929, Ent. Amer. 10: 113 (not Van Duzee)

A large straw-colored species with the transverse brown markings on crown accentuated into an angular black mark on each side between ocellus and eye. Length: ♀, 5 mm., ♂, 4.6 mm.

Genitalia: Figure 18; specimen from S. Margarita, Cal., June 23, 1931, E. D. Ball (USNM).

This species has a distinct spine on the dorsal edge of the male pygofer, visible by external examination. In some respects the spined pygofer resembles that of *symphoricarpae*.

Type: ♀, No. 1806, Colestin, Jackson Co., Oregon, July 31, 1918, E. P. Van Duzee (CASM).

Distribution: More than one hundred specimens examined from California, Oregon, Washington, British Columbia, Idaho, Montana, Utah.

Host Plant: *Symphoricarpus racemosus*.

S. glomerosus (Ball)

Thamnotettix glomerosa Ball, 1910, Canad. Ent. 42: 308.
Athysanus calvatus Ball, 1916, Ent. News 27: 173.
Ophiola glomerosa Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 187.
Ophiola calvata Sleesman, 1929, Ent. Amer. 10: 114.

A broad and inflated front gives this species a distinctive appearance. Some specimens resemble *bullatus* in the reduction on the crown of the transverse dark markings to a black spot against either eye, but remnants of the characteristic *Scleroracus* markings usually can be discerned. The crown has a shallow shelf near the posterior margin. Length: ♀, 5.0 mm., ♂ 4.5 mm.

Genitalia: Figure 9; specimen from Richfield, Utah, Aug. 8, 1930 (USNM).

Type: ♀, Grand Junction, Colorado, July 27, 1900, E. D. Ball (USNM).

Distribution: About twenty-five specimens examined: Arizona (Fredonia); Colorado (Delta, Glenwood Springs, Macedonia); Wyoming (Yellowstone Pk.); Utah (Glenwood, Wellington Elsinore, Oasis, Monroe, Richfield); Washington (Toppenish).

Host Plant: Label data are *Sarcobatus vermiculatis*, *Chrysothamnus speciosus*, *Beta vulgaris* (Richfield, Utah) and *Atriplex rosea* (Delta, Colo.), but probably none is the true host.

S. bullatus (Ball)

Thamnotettix bullata Ball, 1902, Canad. Ent. 34:17.
Frigartus obesus Knull, 1954, Ent. News 65: 37 (new synonymy).

The characteristic markings on the crown may be reduced, causing difficulty in generic placement, but the shape of the aedeagus allows proper association. The large dark spot in the space between ocellus and eye, in combination with the dark basal angles of the scutellum, give pale forms of this species a distinctive appearance. Length: ♀, 5 mm., ♂, 4.2 mm.

Genitalia: Figure 8; specimen from Weed, Calif., 6-27-34, E. D. Ball (USNM).

EXPLANATION OF FIGURES

FIGURES 1–29.—Male genitalia of *Scleroracus*. A, caudal aspect of aedeagus; B, lateral aspect of aedeagus; C, lateral aspect of pygofer and plate; D, dorsoventral aspect of style and connective.

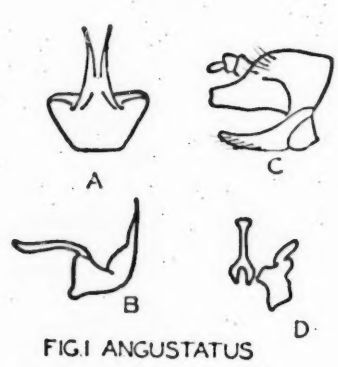


FIG.1 ANGUSTATUS

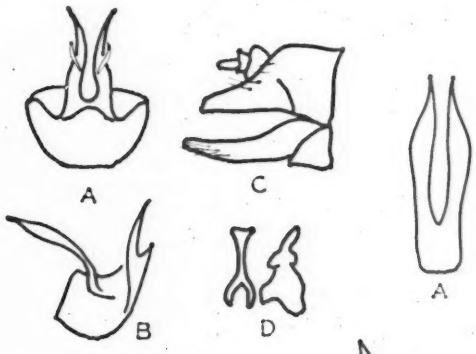


FIG. 2 PALUDOSUS

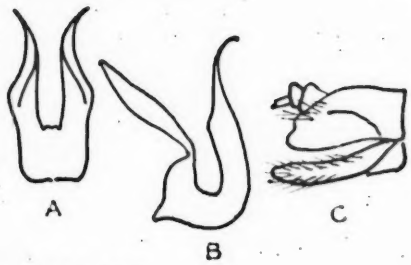


FIG.3 HUMIDUS

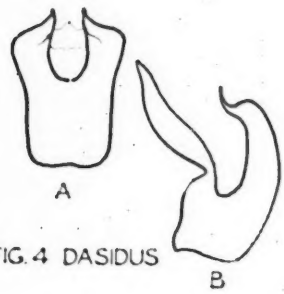
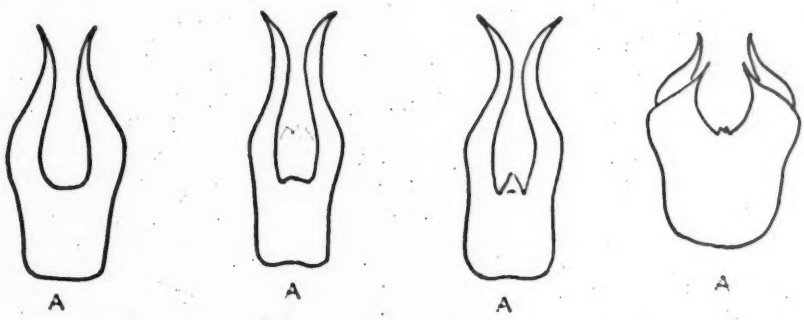


FIG. 4 DASIDUS

FIG. 5 UHLERI



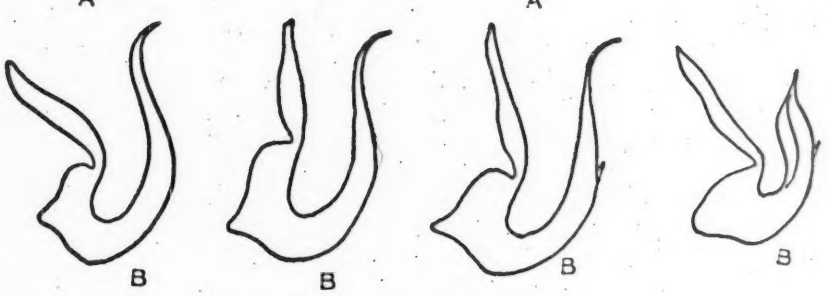


FIG.6 MYRALIS FIG. 7 PLUTONIUS FIG.8 BULLATUS FIG.9 GLOMEROSUS

Type: ♀, Los Angeles Co., Calif., Coquillett (USNM).

Distribution: Fifteen specimens examined from California (Weed, San L. Obispo, San Ardo); Oregon (Dixie, Medford); Washington (Cliffdell, Koloma R., Toppenish); and Idaho (Boise).

Host Plant: Unknown.

S. shastus (Ball)

Athysanus shastus Ball, 1916, Ent. News 27: 174.
Euscelis gentilis Van Duzee, 1925, Proc. Calif. Acad. Sci. 14: 420 (new synonymy).
Ophiola shasta Sleesman, 1929, Ent. Amer. 10: 112.

A large rusty-yellow species with crown rather acutely angled; the transverse lines on crown faded in some specimens, but remnants usually near eyes. Forewing with irregular cross nervures on clavus and occasional supernumerary cells in the outer anteapicals. Length: ♀, 5 mm., ♂, 4.5 mm.

Genitalia: Figure 15; drawn from the type.

Type: ♂, Dunsmuir, Calif. Aug. 13, 1912, E. D. Ball (USNM).

The types of *gentilis* Van Duzee were examined. The holotype ♀ (No. 1802) is labeled "Cazadero, Cal. Sept. 2, 1918". The allotype ♂ (No. 1803) is labeled "near Hobergs, Lake Co., Cal. Aug. 2, 1916," (CASM).

Distribution: Specimens examined from California (Santa Cruz Mts., Yosemite Nat. Park, Davenport, Chico, Castella, Colfax); Oregon (Hood River) and Van Couv. Island.

Host Plant: Unknown.

S. melastigmus Medler

Scleroracus melastigmus Medler, 1955, Ent. News 66: 214.

The heavy transverse band between the eyes posterior to the ocelli, brown-orange on female, black on male, is distinctive. Length: female 4.2 mm., male 4.0 mm.

Genitalia: Figure 17; drawn from the type.

Type: ♂, Red Deer River, Manitoba, Aug. 3, 1937, R. H. Beamer (KUM).

Distribution: Ontario, Manitoba, British Columbia in Canada, and Montana and Colorado in the United States.

Host Plant: Unknown.

S. humidus (Osborn)

Athysanus humidus Osborn, 1915, Maine Agr. Exp. Sta. Bul. 238: 131.
Ophiola humida Sleesman, 1929, Ent. Amer. 10: 112.

A small, slender species readily distinguished by its acutely angled crown, and uniform pale straw color. The crown is usually unmarked; the pronotum and scutellum may have faint brown markings. Length: ♀, 3.5 mm., ♂, 3.2 mm.

Genitalia: Figure 3; drawn from paratype, Orono, Maine, Aug. 5, 1913 (USNM).

Type: ♀, Orono, Maine, Aug. 5, 1913, Osborn (OSUM).

Distribution: Maine; Michigan (Cheyboygan Co., Thompson); Wisconsin. (Ladysmith); Minnesota (Aitken).

Host Plant: A specimen from Thompson, Mich. is labeled: —on *Chamaedaphne*. Recorded by Osborn in bog situations.

S. arctostaphyli (Ball)

Athysanus arctostaphyli Ball, 1899, Ent. News 10: 172.
Ophiola arctostaphyli Sleesman, 1929, Ent. Amer. 10: 111.

A distinctive chestnut brown species with a short, broad appearance, angulate crown and truncated wing, which in female is no longer than tip of ovipositor. Length: ♀, 4 mm., ♂, 3.5 mm.

Genitalia: Figure 23; drawn from paratype, Rist Canyon, Colo. July 13, 1898 (USNM).

Type: ♀, Happy Hollow, Colorado, July 14, 1898 (USNM).

Distribution: A northern species which extends southward in the United States at higher elevations in the Rocky Mountains and the Adirondacks. Specimens examined from Arizona (Kaibab Forest); Colorado (Pagosa Springs, Pingree Park); Nevada (Bunkerville); Montana (Bennett, Butte, Missoula); South Dakota (Piedmont); Minnesota (St. Paul); Manitoba (Churchill, Mafeking, Birch River); Michigan (Cheboygan Co.); Quebec (La Trappe); Maine (Mt. Katahdin 4700-5000 ft.); Vermont (Mt. Mansfield 4000-4450 ft.); New Hampshire (White Mts., Mt. Madison); New York (Mt. McIntyre, 5112 ft., Mt. Marcy 5344 ft.).

Host Plant: Bearberry or Kinnikinnick (*Arctostaphylos uva-ursi*).

S. cacheolus (Ball)

Ophiola striatula var. *cacheola* Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 189.

A dark species, which closely resembles dark forms of *balli* in Colorado and New Mexico localities, but with different internal male genitalia. The species is closely related to *arctostaphyli* in the structure of the aedeagus. However the crown is more blunt and the wing of the female is more slender, extending beyond the tip of the ovipositor. Length: ♀, 4.3 mm., ♂, 4.0 mm.

Genitalia: Figure 22; drawn from paratype, Logan, Ut. Pk., July 9, 1916 (USNM).

Type: ♂, top of Wasatch Range near Logan, Utah, July 9, 1916, Ball (USNM).

Distribution: Many specimens examined from the Rocky Mountain Region: Arizona (Kaibab Nat. Forest, Springervl); New Mexico (Cowles, Cloudcroft, Jemez Spgs., Silver City, Chama); Colorado (Spring Cr. Pass, Little Beaver, Pagosa Springs, Camerons Pass, Muddy Pass, Poudre Riv. Can., Creede, Walden, Durango, Craig, Rockwood, Trinidad); Wyoming (Big Horn Mts., Yellowstone Pk., Anaconda, Bennett, Bozeman); South Dakota (Piedmont); Utah (Richfield).

Host Plant: Unknown.

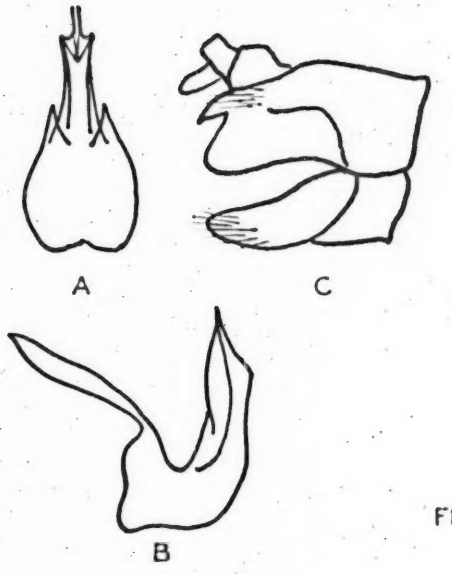


FIG. 10 SYMPHORICARPAE

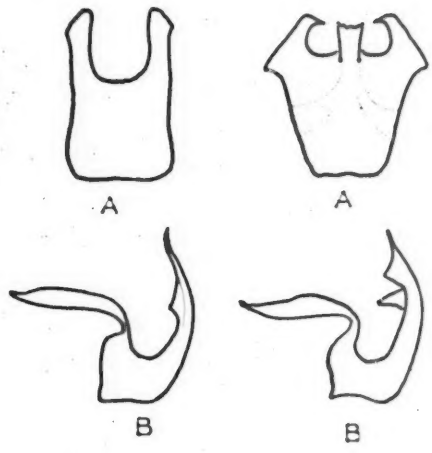


FIG. 11 LUTEOLUS FIG. 12 VACCINII

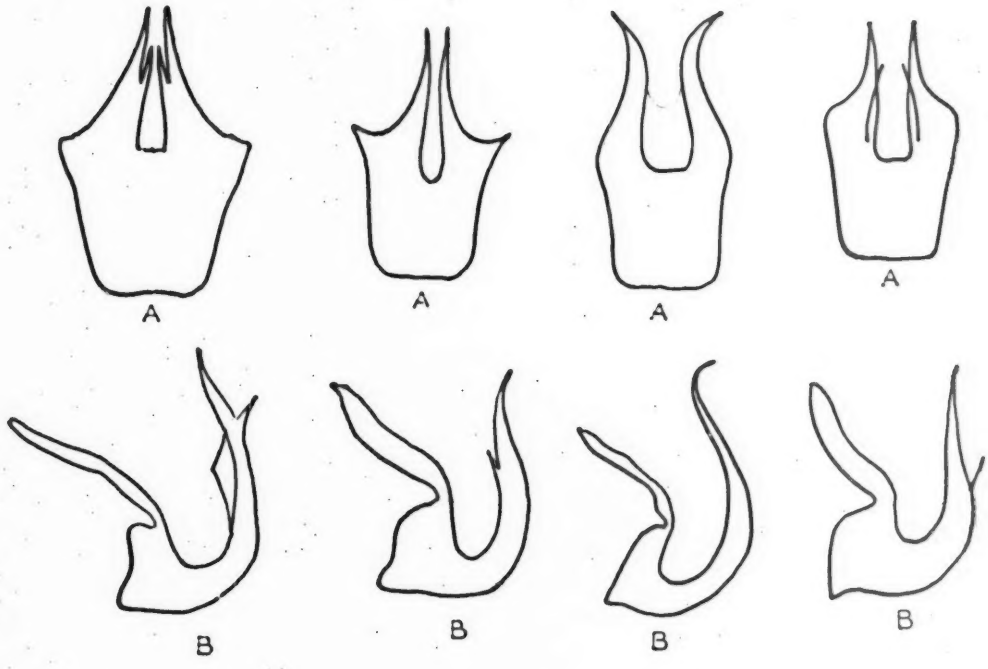


FIG. 13 VARUS FIG. 14 TARAMUS FIG. 15 SHASTUS FIG. 16 BEAMERI

See page 232 for explanation of figures.

S. myralis Medler

Scleroracus myralis Medler, 1958, Pan-Pacific Ent. 34: 14.

A light tan species without distinctive markings on pronotum, scutellum and legs, but at least one distinct brown transverse band posterior to ocelli. Length: ♀, 4.6 mm., ♂, 4.0 mm.

Genitalia: Figure 6; drawn from the type.

Type: ♂, Snyderville, Utah, July 16, 1935, P. W. Oman (USNM).

Distribution: A western species, with distribution recorded only in Utah, Colorado, and Wyoming.

Host Plant: Unknown.

S. comptonianus (Ball)

Ophiola comptoniana Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 189.
Ophiola comptoniana Sleesman, 1929, Ent. Amer. 10: 121.
Ophiola symphoricarpae Medler, 1942, Minn. Agr. Exp. Sta. Tech. Bul. 155: 86. (not Ball).

Species tawny; crown conical and inscribed with light red-brown markings in a scroll-like pattern, blending in varying shades. Length: ♀, 4.5 mm., ♂ 4 mm.

Genitalia: Figure 25; specimen from Salem, N. Y., June 23, on sweet fern, E. D. Ball (USNM).

Type: ♀, Roselle Park, N. J., E. D. Ball (USNM).

Distribution: About 200 specimens examined from the northeastern United States, Michigan, Wisconsin, and Minnesota.

Host Plant: Sweet fern, (*Comptonia peregrina*) and sweet gale (*Myrica gale*).

S. plutonius (Uhler)

Jassus plutonius Uhler, 1877, U.S. Geol. and Geogr. Surv. Terr. Bul. 3: 470.
Ophiola plutonia Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 187.

A dark species, similar to *corniculus* in elongate shape and black markings; but larger, with a distinctive aedeagus and not found in eastern North America. Length: ♀, 4.5 mm., ♂, 4 mm.

Genitalia: Figure 7; specimen from Colo. 2011, C. F. Baker (USNM).

Type: ♀, Clear Creek Canon, (USNM).

Distribution: Alaska (Matanuska, Gulkana); British Columbia (Koslo, Bear Lake); Oregon (Allendale, Hood River); Utah (Richfield); Montana (Bozeman); Wyoming (Yellowstone Pk.); Colorado (Lizard Hole, Little Beaver). The specimen from Dilley, Ore., recorded as *elongatus* by Osborn (1915) probably belongs here.

Host Plant: Unknown, but specimens are recorded from a bog habitat.

S. beameri Medler

Scleroracus beameri Medler, 1958, Pan-Pacific Ent. 34: 14.

A darkly marked species, with pointed crown and relatively long wings: Length: ♀, 4.8 mm., ♂, 4.2 mm.

Genitalia: Figure 16, drawn from the type.

Type: ♂, Hecita, Oregon, July 11, 1935, R. H. Beamer, (KUM).

Distribution: Oregon (Hecita, Florence) and Washington (Rochester, Ft. Lewis).

Host Plant: Unknown.

S. varus (Ball)

Athysanus varus Ball, 1901, Canad. Ent. 33: 5.
Ophiola vara Sleesman, 1929, Ent. Amer. 10: 118.

Species large and robust, usually appearing dark, but some specimens showing a dirty straw-color. Forewing with nervures distinct, the cells mostly filled with fuscous, the first cross vein with a broad patch, which is usually yellow, but sometimes milk-white. Length: ♀, 5.0 mm., ♂, 4.25 mm.

Genitalia: Figure 13; specimen from Leonard, N. Dak., July 25, 1937, R. H. Beamer (KUM).

Type: ♀, Ft. Collins, Colo., 1898 (USNM).

Distribution: A mid-western species. More than 100 specimens examined from Minnesota, Wisconsin, Illinois, Indiana, Colorado, North Dakota, Manitoba, and Ontario (Mer Bleu).

Host Plant: Unknown.

S. osborni (Ball)

Athysanus vaccinii Osborn and Ball, 1902, Ohio Nat. 2:242 (not Van Duzee).
Ophiola osborni Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 190.
Ophiola osborni Sleesman, 1929, Ent. Amer. 10: 120.

This common and widely distributed species is most easily recognized by the color of the legs, which have the tips of the anterior and middle femora and all of the tibiae, orange or yellow. Length: ♀, 5.0 mm., ♂, 4.3 mm.

Genitalia: Figure 24; specimen from Exp. Sta., Ames, Ia., 6-24-97 (USNM).

Type: ♀ Ames, Iowa, E. D. Ball (USNM).

Distribution: Seven hundred specimens examined from many localities. Figure 30 shows the widespread distribution of the species in the United States and Canada according to available records. Southward distribution may be at the higher elevations, e.g., at 1800 feet in Virginia.

Host Plant: No exact record is available. Labels are: blackberry assn. (Fremount, Ind.); *Ribes* (Taos, N. M.); on aspen (Salem, N. Y.); weeds and flowers (Shenandoah Natl. Pk., Va., Alt. 1800 ft.); goldenrod (Babylon, L. I.); high prairie (Ft. Snelling, Minn.).

S. taramus Medler

Scleroracus taramus Medler, 1958, Pan-Pacific Ent. 34: 14.

Species resembling *osborni* in size and obtuse shape of crown, but with fore and middle femora twice-banded with fuscous. This species is best identified on basis of the distinctive internal male genitalia.

Length: female, 5.0 mm., ♂, 4.5 mm.

Genitalia: Figure 14; drawn from the type.

Type: ♂, Richfield, Utah, July 15, 1930, light trap (USNM).

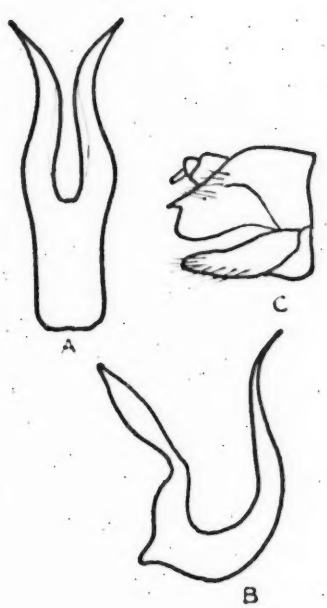


FIG. 17 MELASTIGMUS

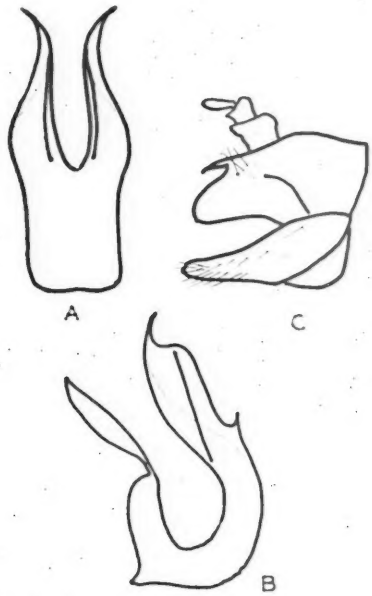


FIG. 18 FINITIMUS

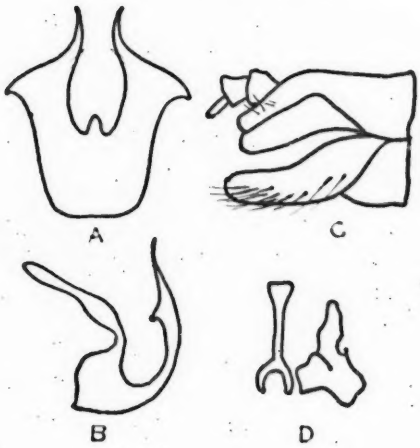


FIG. 19 ANTHRACINUS

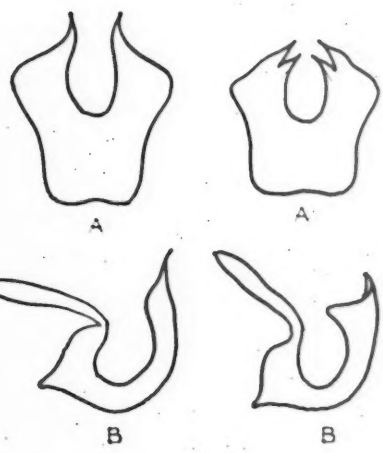


FIG. 20 OMANI FIG. 21 KRYPTUS

See page 232 for explanation of figures.

Distribution: Known only from about a dozen specimens from Utah, Colorado, New Mexico, and Saskatchewan (Saskatoon).

Host Plant: Unknown.

S. dasidus Medler

Scleroracus dasidus Medler, 1955, Ent. News 66: 212.

A light tan species with the general shape of *osborni*, but slightly smaller and with different leg markings. Separated from *balli* by the distinctive aedeagus. Length: ♀, 4.3 mm., ♂, 4.0 mm.

Genitalia: Figure 4, drawn from the type.

Type: ♂, Logan Canyon, Utah, July 26, 1915 (USNM).

Distribution: Examination of over 100 specimens shows a widespread range in western North America. Recorded from Alaska, British Columbia, Washington, California, Idaho, Utah, Montana, Wyoming, Colorado, Saskatchewan, Manitoba, Minnesota, Wisconsin, and Michigan.

Host Plant: Unknown.

S. vaccinii (Van Duzee)

Athysanus striatulus Van Duzee, 1890, Ent. Amer. 6: 134 (not Fallén).

Athysanus vaccinii Van Duzee, 1890, Ent. Amer. 6: 135.

Athysanus striatulus Osborn and Ball, 1902, Ohio. Nat. 2: 242 (not Fallén; in part).

Ophiola striatula Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 188 (not Fallén; in part).

Ophiola striatula Sleesman, 1929, Ent. Amer. 10: 119 (not Fallén).

Ophiola striatula Medler, 1942, Minn. Agr. Exp. Sta. Tech. Bul. 155: 86 (not Fallén).

Scleroracus vaccinii Oman, 1947, Iowa St. Coll. Jour. Sci. 21: 206.

Ophiola striatula DeLong, 1948, Illinois Nat. Hist. Surv. Bul. 24: 281 (not Fallén).

This olivaceous appearing species can be confused with *osborni* in the eastern United States, particularly the darker forms which may have similar coloration of the first pair of legs, but the second pair of legs has a twice-banded appearance. Some specimens have a "yellowish" appearance, the wing veins being yellowed. Length: ♀, 4.0 mm., ♂, 3.8 mm.

Genitalia: Figure 12; specimen from Woodland, N. J., June 18, 1946, on cranberry, W. E. Tomlinson (USNM).

Type: ♂, N. Jersey, J. B. Smith (ISCM), illustrated by Oman (1947, p. 206).

This common bog species has long been misidentified as *striatulus* Fallén. According to Osborn and Ball (1902, p. 243) "Specimens of *striatulus* from Europe (Dr. Melichar) agree with our specimens in every respect, except that in them the central anteapical cell is often divided while in our material this is rarely the case." Ball (1928, p. 188) wrote "The writer has studied examples of *A. striatulus* from five different European sources and finds that they all agree in representing the broad and very variably colored species so abundant on cranberry marshes and similar situations." Sleesman (1929, p. 119) stated that "American forms compared with European forms with which they agree."

Oman (1947, p. 206) illustrated the aedeagus of the lectotype male of *vaccinii* Van Duzee. A similar aedeagus was illustrated by Sleesman (1929, pl. IX) as *striatula*. The aedeagus of *vaccinii* is distinctive, and I have found no counterpart in the limited European material available for my dissections.

Distribution: More than 400 specimens examined; the males being identified by the internal male genitalia. In addition to many localities in the northeastern United States, (Pennsylvania, New Jersey, New York, Massachusetts, and Maine), the species was found in Michigan, Illinois, Wisconsin and Minnesota, and the Canadian Provinces of Nova Scotia, Ontario, and Quebec.

Host Plant: This species is associated with bog plants of the Heath family, Ericaceae, particularly cranberry (*Vaccinium*) and leatherleaf (*Chamaedaphne*). I also examined specimens from dwarf huckleberry (*Gaylussacia dumosa*) and sheep laural (*Kalmia*), collected by H. J. Franklin in Massachusetts.

S. vaccinii is commonly known as the blunt-nosed cranberry leafhopper. It is economically important as the vector of the cranberry false-blossom virus.

S. luteolus (Sleesman)

Ophiola luteola Sleesman, 1929, Ent. Amer. 10: 120.

A yellowish species with faded crown markings. This species is closely related to *vaccinii* (Van Duzee), but distinguished by different internal male genitalia. Length: female 4.4 mm., male 4.3 mm.

Genitalia: Figure 11; specimen from McLean Bogs, Tompkins Co., N. Y., July 21, 1923, J. L. Buys (USNM).

Type: ♂, Wareham, Mass., in collection of D. M. DeLong. The male specimen used for Sleesman's illustration is on a card point with a female, but the internal male genitalia were missing when received for study from D. M. DeLong. Among hundreds of specimens studied in eastern collections only a single male was discovered, which has been used for my illustration.

Distribution: Known only from Wareham, Mass., and McLean bog, New York.

Host Plant: Unknown bog plant, perhaps *Vaccinium*.

S. corniculus (Marshall)

Iassus (?) corniculus Marshall, 1866, Ent. Mon. Mag. 3: 119.

Athysanus instabilis Van Duzee, 1893, Canad. Ent. 25: 284.

Athysanus elongatus Osborn, 1915, Maine Agr. Exp. Sta. Bul. 238: 129.

Ophiola plutonia Ball, 1928, Bul. Brooklyn Ent. Soc. 23: 187 (not Uhler, in part).

Ophiola cornicula Sleesman, 1929, Ent. Amer. 10: 115.

Scleroracus instabilis Oman, 1947, Iowa St. Coll. Jour. Sci. 21: 205.

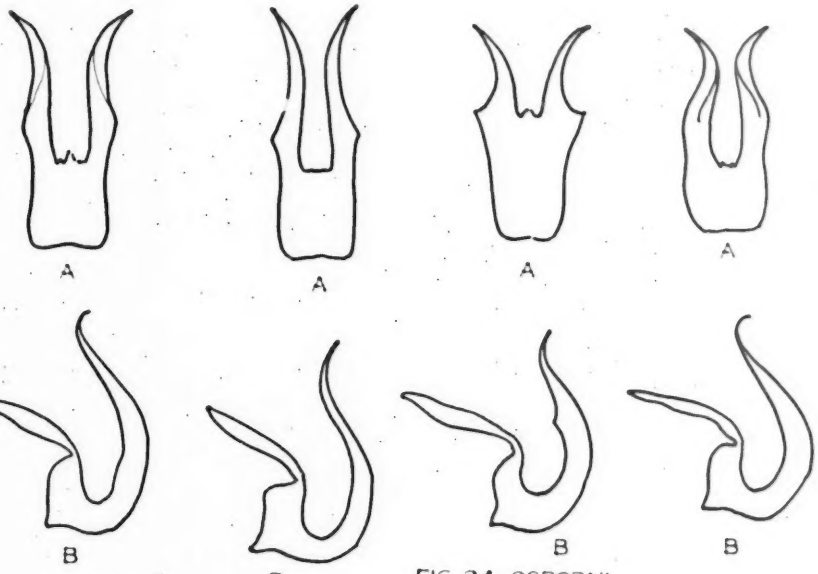


FIG. 22 CACHEOLUS FIG. 23 ARCTOSTAPHYLI FIG. 24 OSBORNI FIG. 25 COMPTONIANUS

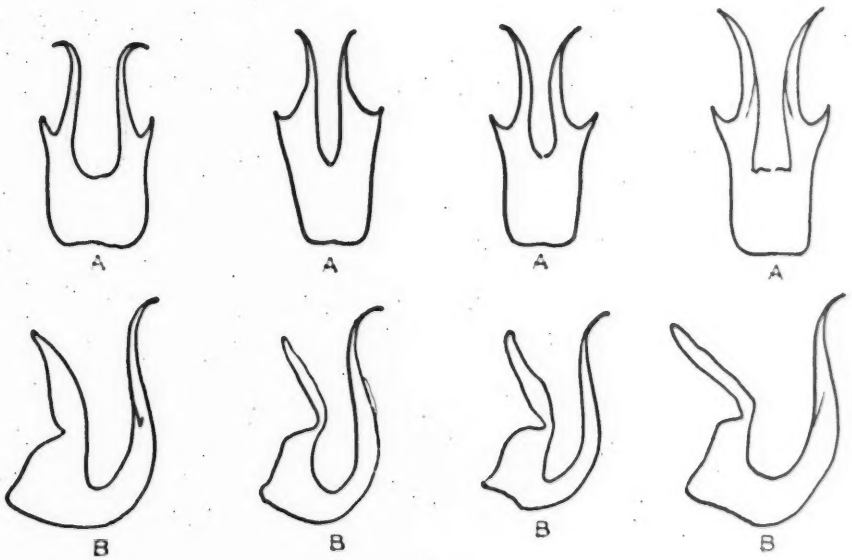


FIG. 26 CORNICULUS FIG. 27 INSTABILIS FIG. 28 ELONGATUS FIG. 29 BALLI

See page 232 for explanation of figures

This is a distinctive, black colored, elongate species, which is heavily marked with black transverse markings on the rather narrow and conically pointed crown. The forewing is long and narrow, giving the species a slender appearance. Length: ♀, 4 mm., ♂, 3.5 mm.

Genitalia: Figure 26; redrawn from a sketch of the type, sent to me by W. E. China.

Type: ♂, Rannoch, Scotland (British Museum, Natural History).

The above synonymy is believed to be correct, since Figure 27, redrawn from the illustration of the type of *instabilis* Van Duzee (Oman, 1947) and Figure 28, drawn from a paratype of *elongatus* Osborn, Orono, Maine (USNM), show close similarity to the aedeagus of *corniculus* Marshall. Also, specimens from Michigan were sent to the British Museum (Natural History) and compared with the type of *corniculus* Marshall by W. E. China. I myself have not examined authentically determined *corniculus* from England, but Sleesman (1929) made a comparison.

A complex of species with a lateral spine on the aedeagus is found both in North America and Europe, including *corniculus* Marshall 1855, *instablis* Van Duzee 1893, *striatulus* Edwards, 1894, *elongatus* Osborn, 1915, *striatulus* Kontkanen, 1949, *intractabilis* Kontkanen, 1949 and *balli* Medler 1958.

Distribution: Specimens examined from many localities in the northeastern United States (Maine, New Hampshire, New York, New Jersey, Pennsylvania, Ohio, Maryland); Michigan, Wisconsin, Minnesota, Colorado, Washington; and in Canada (Quebec, Ontario, Manitoba, British Columbia).

Host Plant: In England, the species feeds on heather, *Calluna vulgaris* and perhaps *Vaccinium* spp. (China informed me by letter that the burning of the heather drove the specimens collected by Marshall on to the *Pteris*.) In North America, the host plant is not definitely recorded, but the association of the species with a bog habitat would suggest host plants in the Ericaceae; probably *Vaccinium*. Osborn (1915) recorded *elongatus* on blueberry.

FIG. 30.—Distribution of *Scleroracus osborni* in North America.

S. balli Medler

Scleroracus balli Medler, 1958, Pan-Pacific Ent. 34: 13.

This species resembles *cacheolus*, *vaccinii*, and *osborni* in its general shape and size, but can be distinguished on the basis of distribution, coloration and characters of the internal male genitalia. Color variation occurs; the typical dark forms intergrade into light colored forms which have considerable reduction in markings. Length: ♀, 4.5 mm., ♂, 4.0 mm.

Genitalia: Figure 29; drawn from the type.

Type: ♂, Estes Park, Colo., July 18, 1935, Oman (USNM).

Distribution: Predominantly at the higher elevations of the Rocky Mountain Region in Colorado and Montana. Also Lake Tahoe, Calif., and Manitoba (Red Deer River, Mafeking, Swan River, Deepdale).

Host Plant: Unknown.

S. angustatus (Osborn)

Athysanus angustatus Osborn, 1915, Maine Agr. Exp. Sta. Bul. 238: 130.

Ophiola angustata Sleesman, 1929, Ent. Amer. 10: 116.

Species slender, with dark marking which contrasts with the lemon-yellow color. Intermediate between *Limotettix* and *Scleroracus*, and possibly this species and *paludosus* should constitute a subgenus. Length: ♀, 4 mm., ♂, 3.25 mm.

Genitalia: Figure 1; drawn from paratype, Mt. Katahdin, Maine, 4700 ft., Aug. 21, 1913 (USNM).

Type: ♀, Mt. Katahdin, Maine, Aug. 22, 1913, 1000–1500 ft. (OSUM).

Distribution: Records from my examination of 60 specimens show a widespread distribution in Alaska, Canada, and the northern United States, including Colorado, Wisconsin, Minnesota, Michigan (Isle Royal), Pennsylvania, New York, New Hampshire, and Maine. Beirne (1956) also gave a general distribution pattern across Canada.

Host Plant: Unknown.

Scleroracus paludosus (Boheman)

Thamnotettix paludosa Boheman, 1845, Handl. Svenska Vet. Akad. 1845: 34.

A narrow, greenish yellow species with black transverse markings on the crown. Forewing smoky brown, the commissure and clavel suture dark brown. Length: female, 5.0 mm., male 4.5 mm.

Genitalia: Figure 2; specimen from Rutland, Sask., July 19, 1940, A. R. Brooks (USNM).

Type: Not determined.

Distribution: Canada, including British Columbia, Alberta, Saskatchewan, and Manitoba.

Host Plant: Unknown.

REFERENCES CITED

Beirne, B. P. 1956. Leafhoppers of Canada and Alaska. Canadian Ent. 88: Suppl. 2. 180 pages.

DeLong, D. M. 1948. The leafhoppers, or Cicadellidae, of Illinois. Bull. Illinois Nat. Hist. Surv. 24: 97–376.

Knull, D. J. 1954. A *Frigartus* from California and an *Erythroneura* from South Dakota. Ent. News 65: 37–39.

Kontakanen, P. 1949. Beitrage zur Kenntnis der Zikadenfauna Finnlands. III. Ann. Ent. Fennici 14: 85–97.

Medler, J. T. 1942. The leafhoppers of Minnesota. Tech. Bull. Minnesota Agric. Expt. Sta. No. 155. 196 pages.

1955. Four new species of *Scleroracus* from the United States and Canada. Ent. News 66: 211–16.

1958. Four new *Scleroracus* from the western United States. Pan-Pacific Ent. 34: 13–16.

Metcalf, Z. P. 1942. A bibliography of the Homoptera. Vol. 1. 886 pages. Raleigh, N. C.

1952. New Names in the Homoptera. Jour. Washington Acad. Sci. 42: 226–31.

Oman, P. W. 1947. The types of anchenorrhynchous Homoptera in the Iowa State College collection. Iowa State Coll. Jour. Sci. 21: 161–228.

1949. The Nearctic leafhoppers. Mem. Ent. Soc. Washington No. 3. 253 pages.

CONCERNING THE APTEROUS ARADIDAE OF THE AMERICAS (HEMIPTERA)

CARL J. DRAKE[1] AND NICHOLAS A. KORMILEV[2]

ABSTRACT

At present 44 species of apterous Aradidae are known from the Western Hemisphere. These are assigned to 12 genera, which are equally divided between the tribes Carventini and Mezirini of the subfamily Mezirinae. 25 species, of 7 genera, are known from Brazil only; 3 species, of 3 genera, have been taken elsewhere in South America; there are 2 species, of different genera, known from Panama, and 2 species of a single genus from the southern U. S. The remaining 12 species, representing 3 genera, are Antillean. Keys to tribes and genera are given, together with a checklist of genera and species.

Unto the present writing, all apterous Aradidae described from the Old and New Worlds belong to the subfamily Mezirinae Oshanin, 1908. We consider Aradidae to be a single family composed of five subfamilies: Calisiinae, Aradinae, Mezirinae, Isoderminae, and Aneurinae.

The genera of apterous aradids of the Americas fall almost equally into the tribes Carventini Usinger (1950: 5) and Mezirini Van Duzee (1916: 16) of the subfamily Mezirinae. As shown in the table below, the apterous forms in these two tribes comprise 44 species (including the new ones described herein) in the Americas and represent 12 genera. The present paper offers original keys to the tribes and genera, characterizes four new species of the tribe Carventini, lists the genera with their respective component species, and gives a bibliography of all the technical papers dealing with the American apterous Aradidae. Specific and generic changes, with their connective

[1]Smithsonian Institution, Washington, D. C.
[2]New York, N. Y.

references, are cited under the species concerned. The types of all new species are deposited as stated. In all micrometer measurements 80 units equal one millimeter.

KEY TO THE TRIBES OF MEZIRINAE

External orifice and channel of metathoracic scent glands situated in front of hind coxae near anterior margin of metapleura, sometimes scarcely perceptible. . . . . Tribe **Carventini** Usinger 1950

External orifice and channel of metathoracic scent glands clearly visible on metapleura, often also apparent from dorsal aspect. . . . . Tribe **Mezirini** Van Duzee 1916

Under revised concepts of the tribes and the described genera, the characters used in the dichotomy above generally are supplemented by another tribal distinction to which thus far only a single specific exception has been noted. In the tribe Carventini the central dorsal plate of the abdomen is formed by solid fusion of four tergites (segments III through VI), while in the tribe Mezirini five tergits (segments II through VI) are fused to form this plate. The one exception occurs in the Neotropical genus *Eunotoplocoris* Kormilev of the tribe Mezirini, *E. ruckesi* Kormilev having the dorsal abdominal plate composed of four fused tergites (III through VI) as in the Carventini.

Kormilev (1953: 237) separated the apterous aradids of the genus *Pictinus* Stål into three distinct groups named respectively "*brasiliensis*," "*teresopolitanus*," and "*usingeri*." In a recent communication, Usinger (letter to Kormilev) stated that he considered "*teresopolitanus*" and "*usingeri*" to represent new genera, and that he was erecting and describing them as such in his forthcoming monograph of the Aradidae. It is our opinion also that these two groups should be given at least subgeneric rank though herein we continue to employ these terms merely as "groups," thus leaving them to Usinger for generic consideration.

KEY TO GENERA OF AMERICAN APTEROUS ARADIDAE OF TRIBE CARVENTINI

1. Eyes stylate 2
— Eyes not stylate 3
2. First antennal segment distinctly longer than head . . . . . **Peggicoris** Drake 1956
— First antennal segment much shorter than head. . . . . **Aglaocoris** Drake & Maldonado 1955
3. Head much wider behind eyes than in front of them; lateral shelves (space between median ridge and each eye) and postocular tubercles deeply excavated . . . . . **Reececus** Drake 1956
— Head narrowed or only slightly widened behind eyes; lateral shelves and postocular tubercles not excavated 4
4. Head slightly subtriangularly dilated just behind eyes and then strongly narrowed in a convex line; lateral borders of pronotum parallel and longitudinally excavated. . . . . **Dihybogaster** Kormilev 1953
— Head narrowed back of eyes in a concave line, at most with only small tubercles just behind eyes; lateral borders of pronotum without such excavation 5
5. Pronotum with a small T-shaped or linear median sulcus; median ridge of meso- and metanotum more or less parallel . . . . . **Glyptocoris** Harris & Drake 1944
— Pronotum without median sulcus; median ridge of meso- and metanotum subtriangular, distinctly dilated backwards . . . . . **Acaricoris** Harris & Drake 1944

KEY TO GENERA OF AMERICAN APTEROUS ARADIDAE OF TRIBE MEZIRINI

1. Scutellum totally absent 2
— Scutellum usually discernible, if not, then metanotum with a double median carina, the latter sometimes fused together though both are still discernible 6
2. Head subquadrate, the postocular part parallel, produced backward as short and blunt or as big and rounded processes . . . . . **Emydocoris** Usinger 1941
— Head not subquadrate, the posterior part narrowed backward in either a straight or a convex line. . 3
3. Apex of head almost reaching to tip of first antennal segment . . . . . **Allelocoris** Drake & Harris 1944
— Head much shorter, the apex at most not extending beyond the basal two-thirds of first antennal segment 4
4. Anterior angles of pronotum produced as long, rounded or as cleft lobes; posterolateral angles of connexiva produced in form of narrow digitate processes, which increase lengthwise from segment II through VII. . . . . **Asterocoris** Drake & Harris 1944
— Anterior angles of pronotum produced into short, rounded lobes; posterolateral angles of connexiva without fingerlike projections, at most with only rounded lobes 5
5. Lateral margins of pronotum converging anteriorly in a convex line; pronotal disc with four (2+2) more or less elevated ridges, the medial pair higher . . . . . **Notoplocoris** Usinger 1941
— Lateral margins of pronotum parallel; pronotal disc with two (1+1) high, rounded tubercles . . . . . **Eunotoplocoris** Kormilev 1957
6. Lateral sides and especially hind border of pronotum neither rimmed nor carinated; pronotal disc broadly depressed in middle, not carinate . . . . . **Pictinus** Stål 1873
— Lateral and especially hind border of pronotum rimmed or carinated; if pronotal disc depressed, then with a fine median, linear depression. 7
7. Anterior angles of pronotum produced forward as small rounded lobes; mesonotum with a double median carina . . . . . Group "**teresopolitanus**" Kormilev 1953
— Anterior angles of pronotum obliquely truncated; mesonotum with double median carina fused together. . . . . Group "**usingeri**" Kormilev 1953

Including the first apterous aradids to be described from the Americas by Usinger in 1941, a total of 44 species have been characterized from the Western Hemisphere. According to the tabulation in Table I, 2 genera and 4 species have been described from North America, 11 genera and 28 species from South America and 6 genera and 12 species from Insular America. It is significant that Brazil is the type locality of 25 species divided among 7 genera. The present interest in the group is reflected by the characterization of more than 70 percent of all of the American species during the past five years.

From such widely scattered, discontinuous, and scanty records as depicted in Table I, it would be

unwise to formulate many conceptions relative to origin, pattern of dispersal, and faunal relationships, especially between insular and continental forms. However, it is interesting to note that all species so far described from the West Indies belong to the tribe Carventini. All of the species are indigenous to the Americas. Host-plant relationships are almost entirely unknown; only the genus *Pictinus* Stål (1873) is known to have macropterous forms. A number of species have been taken from forest litter on the ground by means of a Berlese funnel. Apterous aradids

TABLE 1

APTEROUS ARADID FAUNAE OF THE AMERICAS

	CONTINENTAL					INSULAR			
TRIBE CARVENTINI / GENUS	United States	Panama	Brasil	Peru	Argentina	Cuba	Puerto Rico	Domingo	Guadeloupe
Acaricoris	2	1					3		1
Aglaocoris						1	1	1	3
Dilybogaster			1						
Glyptocoris			7						2
Peggicoris		1							
Reccevius				1					
TRIBE MEZIRINI									
Allelocoris			1						
Asterocoris			2						
Emydocoris			2						
Notoplocoris			5						
Eunotoplocoris				1					
Pictinus			7		1				
Total genera	1	2	7	2	1	1	2	1	3
Total species	2	2	25	2	1	1	4	1	6

have not been recorded as yet from Mexico, Central America (except Panama), Colombia, Venezuela, Ecuador, the Guianas, Bolivia, or Uruguay, nor from many islands of the West Indies.

A brief summary of distributional data and Table 1 shows that the apterous aradids of the Americas are largely tropicopolitan, not many species being recorded outside of the tropics. Only one genus and two species are known to occur in the United States, the rest being inhabitants of the Neotropical realm.

As every genus and almost all of their respective species (including many types) of apterous aradids of North, South, and Insular America are represented in the large collections of the authors, the combined study at first hand of so much material has given us a far better understanding of genera and species and enabled us to straighten out certain nomenclatorial difficulties. The illustrations of generic types of Drake and Maldonado Capriles (1955) have also been most helpful.

Tribe CARVENTINI Usinger 1950

Genus **Acaricoris** Harris & Drake 1944

Acaricoris Harris & Drake 1940: 128.
Eretmocoris Harris & Drake 1940: 132.

The genus *Eretmocoris* Harris & Drake is here suppressed as a synonym of *Acaricoris* Harris & Drake (page priority; new synonymy). The species *E. tatei* Harris & Drake (type species of *Eretmocoris*) and *E. disparis* Drake & Maldonado Capriles are transferred to *Acaricoris*, while the third species *E. insularis* Drake is removed to the genus *Glyptocoris* (new combinations).

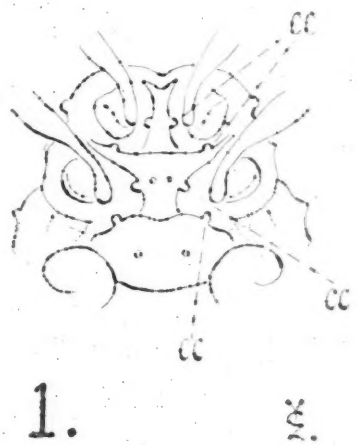


FIG. 1.—*Acaricoris tatei* (H. & D.), circumcoxal tubercles (CC) of the coxal cavities.

Examination of all species of the genus *Acaricoris* (after encrusted coatings were completely removed) has revealed a generic character heretofore overlooked. All members of this genus are provided with paired "circumcoxal tubercles" (new term), as depicted in the ventral view of *A. tatei* (fig. 1). These tubercles are small, rounded, paired, and readily seen after the coxal cavities have been thoroughly cleaned. They are present, as a rule, in the coxal cavities of all three pairs of legs. These tubercles arise scarcely above the inferior edge of the coxal cavities and are directed horizontally toward their respective coxae (fig. 1). The number of pairs of tubercles ranges from one to three (1+1 to 3+3) in both fore and middle coxal cavities, and from none to three pairs (0 to 3+3) in the hind cavities. Circumcoxal tubercles were found in the hind coxal cavities of all members of *Acaricoris* except one species, which was represented in

our collections by a single specimen. As most of the *Acaricoris* species are known from only a few specimens, no attempt has been made to develop formulas for circumcoxal tubercles of the different species. On examining a number of species in various other genera, such tubercles were found only in one species (represented by a single example) of *Glyptocoris*, and the structures were rather poorly developed in this specimen.

Acaricoris barroanus, new species

Small, oblong. Head subquadrate, median length and transocular width subequal, slightly rugulose, a little granulate, with median longitudinal part and lateral shelves on same horizontal level, gradually narrowed at sides behind eyes to neck, there with several small granules behind eyes; antenniferous tubercles short, stout, divergent, finely granulate, subconical; tylus fairly wide, convex and granulate above; juga narrow, with dorsal surface depressed below that of tylus, with apices rounded, rather slender, divergent, and surpassing tylus, the tips extending to basal fourth of antennal segment I; eyes small, exserted, semiglobose. Rostral sulcus wide, scarcely enclosed, transversely rugulose, not quite reaching to neck; rostrum testaceous, scarcely attaining apex of sulcus. Antennal segment I rather stout, granulate, shorter than width of vertex, II very short and slender, III and IV missing. Legs short, brownish testaceous, finely granulate. Pro- and mesothoracic coxal cavities each with two pairs of circumcoxal tubercles; hind coxae with two pairs. Orifice and sulcus of metathoracic scent glands inconspicuous. Length 2.60 mm., width 1.20 mm. (abdomen).

Thorax above with its three divisions and abdominal tergite II all fused together, its lateral sides gradually converging anteriorly and finely granulate; median carina long, rugulose, extending from near base of tergite II anteriorly to pronotal collar, with apex distinctly dilated in front, with one low slender carina each side of median line on mesonotum and three on each side of it on metanotum; raised areas on each side of the median part longitudinally furrowed; pronotum slightly longer than mesonotum, with hind margin convex, with sides strongly roundly narrowed anteriorly, with outer part of fore margin (beyond collar on each side) extending feebly anteriorly beyond collar. Spiracles all lateral and visible from dorsal aspect. Abdominal tergites III through VI completely fused into a subquadrate plate, with the usual pattern of impressed areas and fine ridges, with discal protuberance fairly long, present on tergites IV and V, narrowed apically and connected with the base of plate by a narrow median carina. Body beneath with the three sterna through ventrite III all fused together, the other ventrites separated by transverse sutures.

Holotype (male) and *allotype* (female), Barro Colorado Island, Canal Zone, Panama, Apr.-Oct., 1944, separated out of forest litter by means of a Berlese funnel; in U. S. National Museum. *Paratype*: 1 specimen, taken with type, all collected by James Zetek.

Differs from *A. austeris*, n. sp., by its oblong form, wider and more gradually narrowed pronotum, and the shorter apical lobes of tergite VII.

Acaricoris austeris new species

Small, obovate, reddish fuscous, widest behind middle of abdomen, narrowed anteriorly, finely sculptured, with a small, posteriorly-directed, triangular projection on each side of segment VII. Spiracles all lateral, VII on lateral side of a small angular lobe and VIII (genital) at apical end of a short rounded projection. Length 3.10 mm.; width 1.12 mm. (abdomen).

Head with distance across eyes and median length subequal (0.56 mm.), with dorsal surface of median part and that of longitudinal shelves on about same horizontal level, longitudinally carinate, slowly convexly narrowed behind eyes, there with a tiny tubercle on lateral surface just back of each eye; eyes small, feebly inserted basally; juga slightly surpassing tylus, with the conical ends divergent and slightly turned up; tylus longitudinally convex, with dorsal surface on higher level than that of juga; labial sulcus wide, deep, reaching to neck; labium almost attaining end of sulcus. Segment I of antennae finely granulate, swollen, exceeding apices of anterior process by three-fourths of its length; II short, other segments missing.

Thorax slowly narrowed anteriorly, with lateral sides granulate, with sculpturing composed largely of longitudinal ridges, with all three divisions and first two abdominal segments fused into one solid piece but with transverse sutures in front of and behind mesonotum plainly indicated; pronotum with anteriolateral angles not as strongly rounded as in *A. ignotus*, with a deep median furrow behind collar, broadly shallowly roundly excised in front, two and one-half times as wide at base as median length, the collar narrow, short; mesonotum with median longitudinal ridge, the metanotum with three longitudinal ridges on each side of the median. Abdomen with dorsal tergites III through VI completely fused. Orifice and sulcus of metasternal scent gland inconspicuous. Legs rather short, finely granulate.

Type (male), Guadeloupe, Trois Rivières, West Indies, in Drake Collection (U.S.N.M.). Readily distinguished from *A. ignotus* Harris & Drake by the triangular lobe on each side of abdominal tergite VII. The sculpturing of the dorsal surface of thorax is also different and the anterolateral angles of the pronotum are not so sharply rounded. These same characters also separate it from the new species described below.

Acaricoris clausus, new species

Head subquadrate, transocular width and median length subequal, rugose above; juga longer than tylus, with tips blunt, slightly

divergent, a little upturned and nearly reaching to basal fourth of first antennal segment; eyes small, exserted; lateral shelves on same level as that of median longitudinal part of head, slowly convexly narrowed behind eyes to neck, with two or three tubercles on lateral side behind each eye; neck short, constricted. Rostral groove wide, barely reaching to neck; rostrum reaching to apex of suleus. Antennae rather short, granulate, with the granules larger and more abundant on first two segments, measurements: I, 0.42 mm.; II, 0.20 mm.; III, 0.25 mm.; IV, 0.30 mm.

Thorax with lateral sides slowly convexly converging anteriorly, and more granulate on pro- and mesonotum, with median ridge narrowly furrowed on median line, extending uninterruptedly from base of tergite II to collar, on each side of the ridge widely triangularly depressed, dilated posteriorly and finely longitudinally ridged (four ridges on each side of median ridge behind), with the elevated lobes on each side of median triangular part longitudinally furrowed; pronotum scarcely longer than mesonotum, with median suleus widening in front, excavated on anterior margin for reception of collar, with antero-lateral angles extended forward as far as front margin of collar, separated on each side of median ridge from mesonotum by a transverse suleus running slightly anteriorly; meso- and metanotum together with tergite II all fused into a solid piece, with a transverse furrow on each side of median part between meso- and metanotum. External opening and suleus of metathoracic scent gland not prominent. Spiracles all lateral and visible from above. Abdominal tergites III through VI fused into a solid, subquadrate plate, with a prominent discal elevation, with the usual pattern of ridges and depression on each side; tergite VII elevated posteriorly, highest behind at middle, with a small posterolateral lobe on each side. Meso- and metasternal plates each with a small discal impression. Anterior and middle coxal cavities each with three pairs of circumcoxal tubercles, the hind cavities with only two pairs. Legs brownish testaceous, tuberculate. Entire body slightly shining. Length 3.45 mm.; width (male) 1.62 mm. and 1.90 mm. (female) (abdomen).

Holotype (male) and *allotype* (female), Mayagüez, Puerto Rico, May 1955, J. Maldonado Capriles, taken from forest litter by means of a Berlese funnel, in Drake Collection (U.S.N.M.).

Distinguished from *E. disparis* from Puerto Rico by the more elevated median ridge and produced antero-lateral angles (beyond collar) of pronotum. The discal protuberance of the fused dorsal plate of abdomen is also larger.

Genus **Peggicoris** Drake 1956

Asterocoris (*Peggicoris*) Drake 1956: 326.

Peggicoris, described as a subgenus of *Asterocoris*, is here elevated to the generic level and placed in the tribe Carventini. The central dorsal plate of the abdomen consists of tergites III through VI fused together, and the external orifice and channel of the metathoracic scent gland is concealed. The type species is *P. zeteki* (Drake) from Panama. (New combination).

Tribe Mezirini Van Duzee 1916

Genus **Pictinus** Stål 1873

Pictinus Stål 1873: 140, 145; Kormilev 1953: 287; Usinger 1954: 543.

If the groups "*teresopolitanus*" and "*usingeri*" Kormilev (1953) are removed from the genus *Pictinus* Stål, then only *P. brasiliensis* (Wygodzinsky) of the apterous aradids will be left in the genus. We are, however, describing below a second wingless species of this group, which has the wing-pads more developed than those of *brasiliensis*.

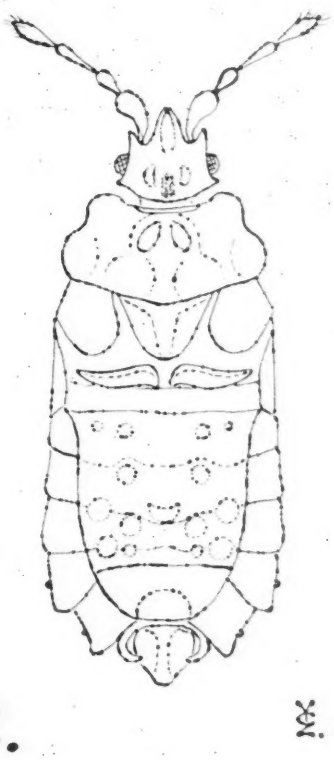


Fig. 2.—*Pictinus brachypterus*, n. sp.

Pictinus brachypterus, new species

(Fig. 2)

Male.—Head finely granulate, with median length and transocular width almost equal (40: 44); anterior process short, slightly tapering, rounded anteriorly, with juga and tylus of equal length, reaching to middle of first antennal seg-

ment; antenniferous tubercles small, parallel, extending to basal third of first antennal segment; eyes moderately large, moderately excerted, semiglobose. Postocular tubercles small, adherent to eyes, projecting laterally slightly beyond outer border of eyes. Vertex finely granulate, lateral shelves slightly convex, each with an ovate, callose spot. Antennae finely granulate, twice as long as head (78: 40), segment I incrassate, clavate, slightly bent near base; II and III tapering towards base, the latter slenderest of all, IV fusiform: measurements: I, 18; II, 14; III, 24; IV, 11. Rostral groove wide and deep, extending to hind margin of head, apex of rostrum reaching to end of sulcus.

Pronotum shorter than width across humeral angles (50: 84); front lobe much narrower than hind lobe (66: 84), the collar set off by an encircling row of very fine tubercles; anterolateral angles rounded and slightly obliquely expanded but neither produced forward nor sideways. Lateral borders of fore lobe parallel, those of hind lobe subparallel, anteriorly rounded and convergent. Hind border of pronotum slightly convexly rounded. Anterior disc with two (1+1) finely granulated elevations, each of which within bears a rounded callose spot; disc between elevations depressed on median line; hind disc slightly depressed at the middle, more rugulosely granulate than that of fore disc. Scutellum triangular, median length shorter than basal width (12: 21), with basal border carinate and slightly concave; disc elevated, finely granulate, with median carina tapering slightly posteriorly. Scent gland openings of metathorax very small, with channel very narrow and linear.

Hemelytra reduced to relatively large scale-like pads that almost touch lateral borders of scutellum and hind margin of metanotum respectively, each pad provided with a U-shaped row of very fine granules. Abdomen longer than the width across segment V (140: 116); tergite I slightly transversely elevated, depressed and almost interrupted at middle; central dorsal plate composed of tergites II through VI more or less fused together, boundary limits between tergites III and IV and between IV and V obsolete. Tergite VII trapezoidal in form, raised posteriorly; connexiva IV through VII with postero-exterior angles slightly elevated and angularly protruding; VII (genital) with lobes long and curved like a hook, with their tips touching the lateral ridges of the hypopygium Hypopygium cordiform, moderate in size, with a median ridge running from base to tip, and two (1+1) short lateral ridges. Spiracles from II through IV ventral, remote from border, those of VI through VIII lateral and visible from above.

General color testaceous with dispersed bright yellow spots; dorsal surface of head in part, of pronotum (not antero-lateral angles) and most of tergum ferrugineous; scutellum, metanotum, postero-exterior angles of connexiva and lateral sides of hypopygium fuscous. Length (male) 3.00 mm.; width 1.00 mm. (pronotum) and 1.35 mm. (abdomen).

Holotype (male), Linha Facao, St. Catarina, Brazil, May 1957, in Drake Collection (U.S.N.M.). Female unknown.

Somewhat allied to *P. brasiliensis* but differs by its smaller size, scutellum with median carina, pronotum distinctly separated into two lobes, scent gland openings small and linear, spiracles of tergite VI lateral and visible from dorsal view.

GENERA AND SPECIES OF AMERICAN APTEROUS ARADIDAE

Subfamily MEZIRINAE Oshanin 1908

Tribe CARVENTINI Usinger 1950

I. Genus **Acaricoris** Harris & Drake 1944
= *Eretmocoris* Harris & Drake 1944
Type species: *Acaricoris ignotus* Harris & Drake.
1. **austeris** Drake & Kormilev, n. sp.; Guadeloupe.
2. **barroanus** Drake & Kormilev, n. sp.; Panama.
3. **clausus** Drake & Kormilev, n. sp.; Puerto Rico.
4. **disparis** (Drake & Maldonado) 1955; Puerto Rico.
5. **floridus** Drake 1957; Florida.
6. **ignotus** Harris & Drake 1944; Louisiana, Mississippi, Georgia, Arkansas.
7. **tatei** (Harris & Drake) 1944; Puerto Rico.

II. Genus **Aglaocoris** Drake & Maldonado 1955
Type species: *Aglaocoris natalii* Drake & Maldonado.
8. **clarkei** Drake 1957; Dominica (B.W.I.).
9. **comes** Drake 1956; Guadeloupe.
10. **cubanus** Drake 1956; Cuba.
11. **invisus** Drake 1957; Guadeloupe.
12. **natalii** Drake & Maldonado 1955; Puerto Rico.
13. **vicinus** Drake 1957; Guadeloupe.

III. Genus **Dihybogaster** Kormilev 1953
Type species: *Dihybogaster incrustatus* Kormilev.
14. **incrustatus** Kormilev 1953; Brasil.

IV. Genus **Glyptocoris** Harris & Drake 1944
Type species: *Glyptocoris sejunctus* Harris & Drake
15. **annulatus** Kormilev 1953; Brazil.
16. **confusus** Kormilev 1953; Brasil.
17. **espiritosantensis** Wygodzinsky 1948; Brazil.
18. **fluminensis** Wygodzinsky 1948; Brasil.
19. **insularis** (Drake) 1957; Guadeloupe.
20. **milleri** Wygodzinsky 1948; Brasil.

21. **plaumanni** Kormilev 1954; Brasil.
22. **sejunctus** Harris & Drake 1944; Brasil.
23. **verus** Drake 1956; Guadeloupe.

V. Genus **Peggicoris** Drake 1956
Type species: *Asterocoris* (*Peggicoris*) *zeteki* Drake
24. **zeteki** (Drake) 1956; Panama.

VI. Genus **Reecеicus** Drake 1956
Type species: *Reecеicus saileri* Drake
25. **saileri** Drake 1956; Peru.

Tribe MEZIRINI Van Duzee 1916

VII. Genus **Allelocoris** Drake & Harris 1944.
Type species: *Allelocoris dryadis* Drake & Harris
26. **dryadis** Drake & Harris 1944; Brasil.

VIII. Genus **Asterocoris** Drake & Harris 1944
Type species: *Asterocoris australis* Drake & Harris
27. **australis** Drake & Harris 1944; Brasil.
28. **sciubarti** Wygodzinsky 1948; Brasil.

IX. Genus **Emydocoris** Usinger 1941
Type species: **Emydocoris testudinatus** Usinger
29. **montanus** Drake 1956; Brasil.
30. **testudinatus** Usinger 1941; Brasil.

X. Genus **Notoplocoris** Usinger 1941
Type species: *Notoplocoris montei* Usinger
31. **mendesi** Wygodzinsky 1948; Brasil.
32. **montei** Usinger 1941; Brasil.
33. **potensis** Drake & Harris 1944; Brasil.
34. **sobrali** Wygodzinsky 1948; Brasil.
35. **triangulatus** Kormilev 1957; Brasil.

XI. Genus **Eunotoplocoris** Kormilev 1957
Type species: *Eunotoplocoris ruckesi* Kormilev
36. **ruckesi** Kormilev 1957; Peru.

XII. Genus **Pictinus** Stål 1873
Type species: *Pictinus cinctipes* Stål 1873
37. **brachypterus** Drake & Kormilev, n. sp.; Brasil.
38. **brasiliensis** (Wygodzinsky) 1948; Brasil.

(Group *teresopolitanus* Kormilev 1953)
39. **dureti** (Kormilev) 1953; Argentina.
40. **intermediarius** Kormilev 1953; Brasil.
41. **montrouzieri** Kormilev 1953; Brasil.
42. **plaumanni** Kormilev 1953; Brasil.
43. **teresopolitanus** (Wygodzinsky) 1948; Brasil.

(Group *usingeri* Kormilev 1953)
44. **usingeri** (Wygodzinsky) 1948; Brasil.

BIBLIOGRAPHY OF AMERICAN APTEROUS ARADIDAE

Drake, C. J. 1956. New Neotropical genera and species of apterous Aradidae (Hemiptera). Jour. Washington Acad. Sci. 46(10): 322–27. 1 fig.
1957. New apterous Aradidae (Hemiptera). Proc. Biol. Soc. Washington 70: 35–40.
Drake, C. J., and **H. M. Harris.** 1944. South American Aradidae (Hemiptera) in the Carnegie Museum. Ann. Carnegie Mus. 30: 39–43.
1944. Two new genera and two new species of apterous aradids from Brasil (Hemiptera). Rev. Brasil. Biol. 4(3): 363–66. 1 fig.
Drake, C. J., and **J. Maldonado Capriles.** 1955. New apterous Aradidae from Puerto Rico (Hemiptera). Jour. Washington Acad. Sci. 45(9): 289–94. 9 figs.
Harris, H. M., and **C. J. Drake.** 1944. New apterous Aradidae from the Western Hemisphere (Hemiptera). Proc. Ent. Soc. Washington 46(5): 128–32.
Kormilev, N. A. 1953. The first apterous aradid from Argentina (Hemiptera). Dusenia 4(2): 125–26. 1 fig.
1953. Notes on Neotropical Aradidae III (Hemiptera). On some apterous Mezirinae from Brazil. Dusenia 4(4–5): 229–42. 1 pl. (11 figs.).
1954. Notes on Neotropical Aradidae IV (Hemiptera). On some apterous Mezirinae from Brazil II. Dusenia 5(3–4): 125–30. 2 figs.
1957. Notes on Neotropical Aradidae (Hemiptera) VII. On some apterous Aradidae in the American Museum of Natural History. Amer. Mus. Novitates No. 1860: 1–7. 4 figs.
Oshanin, B. 1908. Fam. Aradidae. In: Verzeichnis der palaearktischen Hemipteren 1(2): 463–81. (page 478)
Stål, C. 1873. Enumeratio Hemipterorum. 3. Kongl. Svenska Vet.-Akad. Handl. 11(2): 1–163. (page 138).
Usinger, R. L. 1941. Three new genera of apterous Aradidae (Hemiptera). Pan-Pacific Ent. 17(4): 169–81. 3 figs.
1950. The origin and distribution of apterous Aradidae. Proc. 8th Internat. Congr. Ent. Stockholm 1948: 174–179.
1954. A new genus of Aradidae from the Belgian Congo, with notes on stridulatory mechanisms in the family. Ann. Mus. Congo Tervuren in-4°, Zool. 1: 540–43, 6 figs.
Van Duzee, E. P. 1916. Check list of the Hemiptera (excepting the Aphididae, Aleurodidae and Coccidae) of America north of Mexico. xi+111 pages. New York: New York Entomological Society. (page 16)
1917. Catalogue of the Hemiptera of America north of Mexico excepting the Aphididae, Coccidae and Aleurodidae. Univ. California Publs., Tech. Bull., Ent. Vol. 2. xiv+902 pages. (page 137).
Wygodzinsky, P. 1948. Studies on some apterous Aradidae from Brazil (Hemiptera). Bol. Mus. Nac., Rio de Janeiro, N.S., Zool. No. 86: 1–23. 115 figs.

RECENT PUBLICATIONS

Index XV to the Literature of American Economic Entomology, 1955, and the 12th Edition of the Pest Control Directory, Entoma, 1957–1958 are now available. All entomologists need these publications for ready reference.

GROWTH AND FEEDING BEHAVIOR OF LARVAE OF CTENICERA AERIPENNIS DESTRUCTOR (BROWN) (COLEOPTERA:ELATERIDAE) III. EFFECTS OF SEEDS OF CRESTED WHEATGRASS, BROMEGRASS, AND RAPE[1]

G. R. F. DAVIS[2]

Entomology Section, Canada Department of Agriculture Research Laboratory, Saskatoon, Sask.

ABSTRACT

Rapeseed was attractive to these larvae when no choice of food was available, but was less attractive when supplied in combination with the other two foods. Medium-sized larvae gained more weight and survived in greater numbers on rapeseed than on the other foods, which caused a loss in weight. Large larvae maintained their original weight except on crested wheatgrass. They survived in greater numbers on bromegrass, with the mixed diet, or without food than with crested wheatgrass or with rapeseed. The data indicate a nutritional difference between larvae of the two sizes.

In 1955, an estimated 2,065,000 acres of land in Saskatchewan were sown to tame hay and pasture (Evans, 1956). Of this acreage, a substantial portion was sown to bromegrass and crested wheatgrass. The production of bromegrass seed was 4,200,000 lb., almost twice as much as in 1954, and of crested wheatgrass seed, 1,000,000 lb., approximately the same as in 1954. Acreage sown to rape in 1955 was 123,000 acres, nearly four times that of 1954, and 73,800,000 lb. of rapeseed were produced (Evans, 1956). The increased interest in crested wheatgrass, bromegrass, and rape has increased the importance of a twofold problem: the effect of wireworms on these crops and the effects of these crops on wireworm populations. This is a report on the growth and behavior of larvae of *Ctenicera aeripennis destructor* (Brown) reared for 30 weeks on seeds of crested wheatgrass, bromegrass, and rape, provided individually and in combination.

MATERIALS AND METHODS

The procedure was the same as when larvae of this species were reared on carrot slices and seeds of wheat, flax, barley, rye, and alfalfa (Davis, 1957). The ranges of weight were 2.6 to 19.5 mg. and 28.0 to 56.0 mg. for medium-sized and large larvae, respectively, and the averages were 13.4 and 38.4 mg. Three seeds of crested wheatgrass, bromegrass, or rape were added to the soil in each vial when they were provided individually, and one seed of each when they were supplied in combination. No food was added for the control larvae. The tests were replicated four times, each replicate consisting of ten larvae initially.

An arcsine transformation was applied to the data. Differences between effects of various foods on molting, feeding, survival, and change in weight were determined by analysis of variance at the five percent level of significance.

[1]Contribution No. 3706, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

Accepted for publication November 6, 1957.

[2]Associate Entomologist.

RESULTS

The average number of larvae feeding each week was very small (Table I) and of the same order whether the larvae fed on bromegrass, crested wheatgrass, rape, or a combination of the three. When the three foods were provided together, larvae of both sizes fed on a single food in over 85 percent of the instances of feeding. When more than one of the three foods were eaten, medium-sized larvae fed on a combination of crested wheatgrass and bromegrass in six percent of the instances, rape and bromegrass in three percent, and crested wheatgrass and rape in one percent. In no case did they attack all three seeds. When large larvae fed on more than one of the three foods available, they ate a combination of crested wheatgrass and bromegrass in nine percent of the instances, rape and bromegrass in three percent, and crested wheatgrass and rape in one percent. They fed on all three seeds in one percent of the instances of feeding.

Medium-sized larvae molted equally frequently on all foods (Table I). However, fewer large larvae molted each week when no food was provided than when crested wheatgrass, rape, or the combination of the three seeds was supplied. The number of larvae molting in any week did not influence the number feeding, except when medium-sized larvae were reared on rape. In this case, the number of larvae feeding increased proportionately with an increase in the number molting (Table I).

Larvae of the two sizes were almost identical in feeding behavior in relation to molting. During the week before that in which molting occurred, medium-sized larvae fed in only six percent of the cases; large larvae, in five percent. Both sizes fed in 21 percent of the cases during the week after molting. Only medium-sized larvae molted and fed during the same week, and only in one percent of the cases.

Medium-sized larvae gained weight with rape and lost weight with bromegrass, crested wheatgrass, and a combination of the three foods

(Table II). This loss in weight was of the same order as obtained when no food was added to the soil. Large larvae maintained their weight under all conditions of rearing except when crested wheatgrass was supplied as food (Table II). In this case, they lost more weight than when no food was added to the soil.

Medium-sized larvae survived very poorly on all foods. Only as many survived on bromegrass and on crested wheatgrass as when they were not supplied with food, but more medium-sized larvae survived on rape or on the combination of three foods (Table II). On bromegrass, two medium-sized larvae survived for 30 weeks in one replicate and all died by 20, 23, and 27 weeks in the other three replicates. On crested wheatgrass, only one larva survived in each of two replicates for 30 weeks and all died in each of the other two replicates within 20 and 25 weeks, respectively.

Large larvae survived equally well with rape, bromegrass, the combination diet, and without food. Fewer survived when they were provided with crested wheatgrass than when no food was added to the soil (Table II).

DISCUSSION

The most outstanding result of this study was the extremely low survival of medium-sized larvae. Although more survived on rapeseed than on bromegrass or on crested wheatgrass, only as many survived as on rye, the poorest of a number of other natural foods (Davis, 1957). Large larvae survived as well on rapeseed, on bromegrass, or on a combination of the three seeds as they did on carrot slices, wheat, flax, barley, rye, or alfalfa seed (Davis, 1957). However, only half as many survived on crested wheatgrass as on the poorest food of the previous investigation.

The difference in survival between these two investigations was probably not caused by any factor other than the food provided. It is unlikely that the two groups of larvae differed in viability, because larvae of both sizes survived equally well in the same type of soil without food as they did in previous work (Davis, 1958).

Because of the low survival of medium-sized larvae on crested wheatgrass and on bromegrass, calculation of change in weight was difficult. In

TABLE I

AVERAGE WEEKLY PERCENTAGES (ANGULAR TRANSFORMATIONS) OF SURVIVING MEDIUM-SIZED AND LARGE LARVAE OF *C. a. destructor* FEEDING AND MOLTING WITH SEEDS OF CRESTED WHEATGRASS, BROMEGRASS, AND RAPE, PROVIDED INDIVIDUALLY AND IN COMBINATION, AND COEFFICIENTS OF REGRESSION OF INCIDENCE OF FEEDING ON INCIDENCE OF MOLTING

Food	Medium-sized Larvae			Large Larvae		
	Feeding	Molting	Coeff.	Feeding	Molting	Coeff.
Bromegrass	23 9	11 7	−0 1091	27 6	12 2	0 2568
Crested Wheatgrass	21 2	13 2	0 0576	22 7	12 9	−0 2158
Rape	19 4	12 5	0 7718*	24 7	14 1	0 5723
Combination	19 3	13 7	0 3323	24 5	13 2	0 3788
No food		11 9			9 5	
L.S.D. at 5% level					2 8	

*Significant at 1% level.

TABLE II

AVERAGE CHANGES IN WEIGHT IN MILLIGRAMS PER MILLIGRAM OF INITIAL WEIGHT AND PERCENTAGES (ANGULAR TRANSFORMATIONS) OF MEDIUM-SIZED AND LARGE LARVAE OF *C. a. destructor* SURVIVING ON SEEDS OF CRESTED WHEATGRASS, BROMEGRASS, AND RAPE, PROVIDED INDIVIDUALLY AND IN COMBINATION

Food	Medium-sized Larvae		Large Larvae	
	Change in Weight	Survival	Change in Weight	Survival
Rape	+0 10	31 4	−0 05	51 0
Bromegrass	−0 36	6 7	−0 02	56 8
Crested Wheatgrass	−0 58	9 2	−0 32	23 7
Combination	−0 36	22 7	+0 09	76 7
No food	−0 47	0 0	−0 03	62 7
L.S.D. at 5% level	0 42	16 9	0 15	22 6

these cases, the length of the survival period was used rather than 30 weeks. This may have introduced some error into the calculations; however, it was not evident when these weights were compared with others obtained with rape, with the combination, or without food.

Although rape has been listed as a crop resistant to wireworm attack (Cameron, 1939; Davidson, 1941; Granovsky, 1952), larvae of *C. a. destructor* reared in the laboratory fed as frequently on it as on the other seeds when each was provided alone. However, few were attracted to rape when the two other seeds were present. This decrease in attractiveness of rape in combination with the other seeds may explain in part its resistance in the field, where many other plants and seeds are available as food to the wireworm larvae.

The feeding behavior of larvae during the week of molting, the week before, and the week after differed from that observed when carrot, wheat, flax, barley, rye, or alfalfa was supplied (Davis, 1957). Fewer larvae fed on crested wheatgrass, bromegrass, or rape during these periods than on the other six foods. Because of the low level of feeding throughout the investigation (Table I), it is doubtful that these results indicate anything other than a low attraction of the foods to wireworm larvae.

Some indication of a difference in nutritional requirements of larvae of different sizes was obtained in other work (Davis, 1958). The results of the present study support this suggestion. Medium-sized larvae gained weight and survived in greater numbers on rapeseed than on the other foods; large larvae maintained their original weight under all conditions except with crested wheatgrass, and survived in greater numbers with bromegrass, with a mixed diet, and without food than with crested wheatgrass or rape.

REFERENCES CITED

Cameron, A. E. 1940. Insect and other pests of 1939. Trans. Highland Agric. Soc., Scotland 52: 91–115. Biol. Abstr. (E) 15: 1451.

Davidson, R. 1941. What can be done against wireworms? Farmer and Stock Breeder 55: 620.

Davis, G. R. F. 1957. Growth and feeding behavior of larvae of *Ctenicera aeripennis destructor* (Brown) (Coleoptera: Elateridae). I. Effects of carrot slices and seeds of wheat, flax, barley, rye, and alfalfa. Ann. Ent. Soc. America 50: 578–81.

1958. Growth and feeding behavior of larvae of *Ctenicera aeripennis destructor* (Brown) (Coleoptera: Elateridae). II. Effects of sterilized flax seed and sterilized soil. Ann. Ent. Soc. America 51: 164–7.

Evans, E. H. 1956. Annual report of the supervisor of statistics. *In*: Fifty-first annual report of the Department of Agriculture of the Province of Saskatchewan for the twelve months ended March 31, 1956. (pp. 20–52).

Granovsky, A. A. 1952. How to control wireworms. Minnesota Agric. Ext. Folder 170.

DIFFERENTIAL AMOUNTS OF MATERIAL TAKEN UP BY FOUR BIOTYPES OF CORN LEAF APHIDS FROM RESISTANT AND SUSCEPTIBLE SORGHUMS[1]

M. D. PATHAK[2] AND REGINALD H. PAINTER[3]

Kansas State College, Manhattan

ABSTRACT

Measurement was made of the differential amounts of the plant material taken by individuals of four biotypes of the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), from resistant Piper Sudan 428–1 and susceptible White Martin sorghums. All the biotypes gained significantly more weight on susceptible plants than on resistant plants, and also had reduced fecundity on resistant plants. Weight lost on resistant plants was significantly less than the loss when the aphids were kept without access to food. Biotype KS–2 differed from others in its ability to take significantly more material from the resistant plants, on which it also had a greater fecundity than any of the others. The aphids, after being kept overnight without food, took some material from resistant plants in their first three hours of feeding, but lost weight later. In contrast, the fecundity of the biotypes and the amount of plant material taken were not positively related on susceptible plants, where biotypes taking in the most material reproduced the least.

The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is at times a serious pest of barley, corn, and sorghum. Howitt and Painter (1956) tested many of the varieties of sorghums available in the United States for their reactions to corn leaf aphids and reported Sudan type sorghums to be consistently more resistant. A single plant of Piper Sudan 428–1 was found to be highly resistant to the general population of aphids used

[1]Contribution No. 699, Department of Entomology, Kansas Agricultural Experiment Station, Manhattan. Supported in part by National Science Foundation Grant No. 2098. A portion of a dissertation to be presented by M. D. Pathak in partial fulfillment of the requirements for the degree Doctor of Philosophy in Entomology at Kansas State College. Accepted for publication November 26, 1957.

[2]Graduate Research Assistant.

[3]Professor and Entomologist.

in their tests. Later, Cartier and Painter (1956) reported that some aphids from the general population were able to develop small colonies on 428-1 plants. They isolated this population from the general population of aphids and named it biotype KS-2. A representative colony from the remaining population was termed KS-1. KS-2 had a greater survival capacity and higher fecundity on resistant Sudan plants when compared with aphids of KS-1; weight loss also occurred when KS-1 was caged on resistant plants.

Some exploratory studies during the present work revealed the presence of at least two additional biotypes, named KS-3 and KS-4. Details of their origin and other distinguishing characters

FIG. 1.—Arrangement of the rectangular plastic cages used for feeding tests of the corn leaf aphids. Leaves, passing through gaps scraped from the side walls of the cages, were fastened to the bottom with Scotch-tape strips. Cellucotton placed along the gaps protected the leaves from injury by the scraped walls of the cages.

will be reported in another paper. This study measures the amount of plant liquids taken in by individual aphids of different biotypes during a definite period of feeding, using both resistant and susceptible plants.

MATERIALS AND METHODS

Experiments were conducted in a greenhouse at an average temperature of approximately 70° F. Stock cultures of the four biotypes were maintained on Spartan barley plants grown in pots and caged separately in cellulose nitrate cages with tops covered with nylon-orlon cloth and each provided with four nylon-orlon-covered windows. Last instar nymphs of apterous aphids were selected from the stock cultures and were caged on other Spartan barley plants in cellulose nitrate cages or cages made from dialyzing tubing with nylon-orlon-covered windows for ventilation. The following day adults were selected from these cages for feeding tests, which permitted use of aphids of approximately the same age. The aphids were anaesthetized with carbon dioxide and then weighed on a Roller-Smith micro-torsion balance having a range from .002 to 5 mg. and a sensitivity of .002 mg. Each aphid was then caged in a transparent plastic box $2\frac{7}{8}'' \times 2'' \times \frac{3}{16}''$, through which leaves were passed. The leaves were fastened to the bottom of the cages by narrow Scotch tape strips. A gap somewhat thicker than the thickness of the leaf and equal to its width was scraped from the side walls of the cages to permit passage of the leaf. Cellucotton was placed in this gap to protect the leaves from injury and to prevent the escape of the aphids. The boxes were mounted on a circular wire frame around the plants (Fig. 1). The White Martin plants were seed-propagated; the Piper Sudan 428–1 plants were cuttings from a single plant.

The aphids were kept from food for about 15 hours, weighed, then caged in these boxes and given an opportunity to feed for 3 hours. Then they were removed from the cages, reweighed and recaged. The aphids were weighed again after a subsequent 24 hours of opportunity for feeding.

RESULTS

Preliminary tests showed that the aphids responded more consistently in the amount of the plant liquid intake when they were kept without food for a period of 14 to 16 hours and then allowed to feed for 3 hours. In other tests where aphids were kept without food, all the biotypes lost significantly more body weight than when caged on either the resistant or the susceptible sorghums, indicating that some feeding occurred even on the highly resistant 428–1 plant cuttings (Table 1).

The biotypes did not differ significantly in the amount of material taken from the White Martin plants with the exception of KS–1 and KS–3 (% gain, 11.84 and 6.10) after feeding for 3 hours. Significant differences in this respect did occur in all except KS–1 and KS–4 on 428–1 plants at the end of 3 hours. KS–2 gained significantly more weight on 428–1 plants than any of the other biotypes. KS–3 also showed some gain in weight, but biotypes KS–1 and KS–4 showed consistent losses in weight. There was no significant difference between the amount of material taken in by biotype KS–2 from White Martin and 428–1 plants after 3 hours of feeding but the other three biotypes took significantly more material from the White Martin plants. All the individual aphids of KS–2 gained weight on 428–1 plants, while among other biotypes a few individuals gained weight but most lost weight. These results occurred repeatedly in additional tests.

At the end of 24 hours of feeding, all but KS–2 individuals lost weight. It appears that 428–1 plants may have some repellent action to all

TABLE 1

LOSS OR GAIN IN WEIGHT OF 10 APHIDS FROM EACH OF FOUR BIOTYPES OF CORN LEAF APHIDS AFTER 3 AND 24 HOUR FEEDING PERIODS ON TWO SORGHUMS. APHIDS WERE DEPRIVED OF FOOD OVERNIGHT PRIOR TO FEEDING. MANHATTAN, KANSAS, 1957

Biotype*	Average Percent Loss or Gain After					
	3 Hours of Feeding on			24 Hours of Feeding on		
	White Martin	428–1	Check*	White Martin	428–1	Check*
KS–1	+11.84	−2.55	−8.75	+19.96	−10.05	−16.44
KS–2	+8.98	+5.96	−6.25	+14.06	+7.25	−13.04
KS–3	+6.10	+1.82	−5.73	+10.38	−2.00	−12.56
KS–4	+9.78	−2.18	−10.06	+14.04	−6.74	−18.05

L. S. D. at 5% level for 3 hours of feeding, 4.19; for 24 hours, 6.06.

*Aphids kept in glass vials without food or water.

biotypes, but since some food was taken it appears that it was necessary for the aphids to taste the plant sap to detect the repellent. Although KS-3 lost some weight on 428-1 plants, it took significantly more plant material than either KS-1 or KS-4. KS-1 and KS-4 did not show a significant difference in the amount of food taken in from 428-1 plants. When kept without food, check aphids of KS-2 and KS-3 lost comparatively less weight than KS-1 and KS-4.

Table 2 gives results secured when aphids were taken directly from the culture plants to study their feeding response when food was available before conducting tests otherwise identical to those previously described. A striking difference was that KS-3, which gained weight on 428-1 in its first 3 hours of feeding when deprived of food previously (+1.82, Table 1), lost weight when taken directly from culture plants (−2.84, Table 2). This suggests that the starved aphids fed on the 428-1 plants because of hunger. In these tests (Table 2), as well as when aphids were starved (Table 1), KS-2 took significantly more food than any of the other biotypes from 428-1 plants and there was again no significant difference between the amounts of food taken by KS-2 on 428-1 and White Martin plants after 3 hours of feeding. In Table 2, KS-1, KS-3, and KS-4 did not differ significantly in the amount of food taken either from White Martin or 428-1 plants. In this test KS-4 took significantly more food from White Martin plant than KS-2. In other respects the results of this non-starvation test were similar to that described in Table 1.

This non-starvation test was also extended for another 24 hours. On 428-1 plants, KS-2 took significantly greater amounts of food than other biotypes, and KS-3 took significantly more than KS-1. There was no significant difference between biotypes KS-1 and KS-4 and between biotypes KS-3 and KS-4 on 428-1 plants. On White Martin plants, KS-4 took more food than KS-2 and KS-3 but there were no significant differences between biotypes KS-1, KS-2, and KS-3. The records from unfed check aphids of all biotypes were similar in Tables 1 and 2.

Representative results of fecundity studies of the various biotypes after feeding on the two sorghums are given in Tables 3 and 4. KS-1, KS-2, and KS-3 reproduced at about the same rate but KS-3 had higher fecundity rate than KS-1 on White Martin. KS-2 had the highest fecundity on 428-1 plants. Biotype KS-3 had greater fecundity than biotypes KS-1 and KS-4 on 428-1 plants but reproduced at a lower rate than biotype KS-2. The fecundity of all the four biotypes was higher on White Martin plants than on 428-1 plants.

KS-2 reproduced about half as fast on 428-1 plants as on White Martin plants. When this difference in reproduction is compared with the amount of food intake recorded in Tables 1 and 2, it is evident that although KS-2 did not differ significantly in the amount of food taken from White Martin and 428-1 plants during the first 3 hours of feeding, there was a significant difference in the amounts of food taken after 24 hours of feeding when KS-2 took twice as much food from White Martin plants as from 428-1 plants. This is also true of biotype KS-3, which took more food than KS-1 and KS-4, and also reproduced at a higher rate than these biotypes on 428-1 plants. The amount of food taken and the fecundity are not positively correlated with biotype fecundity on White Martin plants. Although biotype KS-1 and KS-4 took more food than KS-2 and KS-3, in fecundity KS-1 and KS-4 were surpassed by the biotypes KS-2 and KS-3.

TABLE II

Loss or Gain in Weight of 10 Aphids From Each of Four Biotypes of Corn Leaf Aphid After 3 and 24 Hours of Feeding Periods on Two Sorghums. Aphids Were Not Deprived of Food Prior to Feeding. Manhattan, Kansas, 1957

Biotypes	After 3 Hours of Feeding on			After 24 Hours of Feeding on		
	White Martin	428-1	Check*	White Martin	428-1	Check*
KS-1	+3 24	−1 68	−5 36	+13 70	−7 30	−16 63
KS-2	+2 61	+0 72	−3 84	+12 19	+4 75	−11 03
KS-3	+4 76	−2 84	−3 68	+11 69	−1 85	−12 72
KS-4	+5 08	−3 03	−5 91	+17 50	−4 92	−14 39

L. S. D. at 5% level for 3 hours of feeding, 2.33; for 24 hours, 4.36.

*Aphids kept in glass vials without food or water.

DISCUSSION

The reduced fecundity of all the four biotypes on Piper Sudan 428-1 compared to White Martin, as also shown by Cartier and Painter (1956), suggested the possibility of a basic difference between these two hosts. Additional evidence is

TABLE III

FECUNDITY[a] OF SINGLE VIVIPAROUS FEMALES OF THE FOUR BIOTYPES OF CORN LEAF APHIDS ON WHITE MARTIN AND PIPER SUDAN 428-1 PLANTS. MANHATTAN, KANSAS, 1956

PLANT	KS-1	KS-2	KS-3	KS-4
White Martin	12 5	15 4	17 3	14 3
428-1 plant (Piper Sudan)	1 2	7 3	3 6	0 4

L.S.D. at 5% level for White Martin = 4 2
" " " " " 428-1 = 2 1

[a]Average nymphs produced, based on 10 replications, each aphid caged for 10 days.

furnished by the inability of some aphids to take enough materials from 428-1 plants to keep up their body weights.

KS-1, KS-3, and KS-4 showed a consistent loss in their body weights when caged on 428-1 plants. This suggests that KS-2 could feed equally well on both resistant and susceptible plants. But the KS-2 aphids took significantly more material from White Martin than 428-1 plants after 24 hours of feeding. The aphids of the biotype KS-2 also reproduced about half as fast on 428-1 plants as they did on White Martin plants. Thus the ability of the KS-2 aphids to take up more material from 428-1 plants than did other biotypes contributed to their ability to produce young when feeding on such plants.

On White Martin plants the amount of plant material taken did not show a direct relation to the fecundity of the biotypes. KS-1 and KS-4 took more plant material than other biotypes but still had less fecundity. This suggests some physiological difference between the various biotypes in their ability to utilize the plant material taken in from White Martin plants. A

TABLE IV

SIGNIFICANT AND NON-SIGNIFICANT DIFFERENCES IN FECUNDITY BETWEEN THE FOUR BIOTYPES OF CORN LEAF APHIDS DURING FEEDING ON WHITE MARTIN AND PIPER SUDAN 428-1 PLANTS. MANHATTAN, KANSAS, DECEMBER 1956

BIOTYPES	BIOTYPES						WHITE MARTIN VS. 428-1
	KS-1 on		KS-2 on		KS-3 on		
	White Martin	428-1	White Martin	428-1	White Martin	428-1	
KS-1							*
KS-2	ns	*					*
KS-3	*	*	ns	*			*
KS-4	ns	ns	ns	*	ns	*	*

ns = non-significant difference.
* = significant difference at 5% level or above.

plants. These biotypes had also reduced fecundity on 428-1 plants. This appears to indicate that the reduced fecundity of these biotypes on 428-1 plants was due to the inability of the aphids to take enough plant materials to reproduce or even to maintain their body weights. This inability of the aphids to take up enough plant materials might be because they either could not or would not feed on 428-1 plants. Histological studies on the feeding of these biotypes now being made should furnish further information.

KS-2 can be distinguished from others by its taking up significantly more plant materials from 428-1 plants than the other biotypes. KS-2 during its first 3 hours of feeding did not show any significant difference in the amount of plant materials taken in from White Martin and difference in the quality of the sap of the White Martin and 428-1 plants is also suggested.

KS-2 and KS-3 might be considered more hardy because of their ability to lose comparatively less body weight than the other biotypes when kept without food.

REFERENCES CITED

Cartier, J. J. and **Reginald H. Painter.** 1956. Differential reactions of the two biotypes of corn leaf aphids to resistant and susceptible varieties, hybrids and selections of sorghums. Jour. Econ. Ent. 49: 498–508.

Harrington, C. D. 1945. Biological races of the pea aphid. Jour. Econ. Ent. 38: 12–22.

Howitt, A. J., and **Reginald H. Painter.** 1956. Field and green-house studies regarding the sources and nature of sorghum (*Sorghum vulgare* Pers.) resistance to the corn leaf aphid, *Rhopalosiphum maidis* (Fitch). Kansas Agric. Expt. Sta. Bull. 82. 38 pages.

ACID AND ALKALINE PHOSPHATASES IN HOUSE FLIES OF DIFFERENT AGES[1]

ROY J. BARKER AND B. H. ALEXANDER
Entomology Research Division, Agr. Res. Serv., U.S.D.A.

ABSTRACT

The activity of acid and alkaline phosphatases was determined in house flies of different ages. Analyses were based on the hydrolysis of *beta*-naphthol phosphate. Acid phosphatase activity was highest in eggs and puparia. In adults, activity in females was greater than in males, but this finding does not seem to be associated with the longer life span of the female. Alkaline phosphatase activity was highest in 2-day-old larvae.

The phosphatase activity of 2- to 3-day-old house flies has been found to be significantly higher in females than in males (Alexander *et al.* 1958). Since the females live longer than the males (Rockstein 1956), the relationship of this activity to aging is of interest. The activity of acid and alkaline phosphatase was determined on all stages of flies in 1-day age increments.

PROCEDURE

House flies (*Musca domestica* L.) of a 1948 NAIDM strain were reared by the Peet-Grady method (C.S.M.A. 1955) except that adults were fed 5% sucrose solution. Several generations were sampled. The number of tests depended upon which ages were conveniently available.

Phosphatase activity was determined by a modification of the method of Seligman *et al.* (1951),[2] which measures *beta*-naphthol liberation from sodium *beta*-naphtholphosphate. Substrates were prepared daily by mixing 55 ml. of aqueous sodium *beta*-naphtholphosphate solution (50 mg. in 250 ml.) with 55 ml. of appropriate buffer. For determining acid phosphatase, an acetate buffer was made by diluting 0.2 *N* acetic acid with 0.2 *M* sodium acetate to obtain pH 4.8; for alkaline phosphatase, a veronal buffer was prepared by diluting 0.1 *M* sodium diethylbarbiturate with 0.1 *N* hydrochloric acid to pH 7.5.

Assays were grouped into duplicates of 10 samples each for acid and alkaline phosphatase. For each series 5 ml. of substrate was placed in each of 22 test tubes. To one tube in each series was added 10 μg. of *beta*-naphthol in 1 ml. of water; this was the standard. One tube with substrate alone served as a blank. About 100 mg. of flies (usually four adults or pupae) were pulverized with a Tenbroeck tissue grinder and suspended in 10 ml. of iced distilled water. These suspensions were centrifuged 4 minutes at moderate speed, then filtered through S&S No. 588 paper. A 0.2-ml. aliquot of the filtrate was added to the acid substrate, and 1 ml. to the alkaline substrate. Within 1 hour after the flies were pulverized, breis were incubated for 1 hour at 37° C. During incubation a tetrazotized diorthoanisidine dye was prepared by dissolving 0.2 gm. of Dupont's Naphthanil diazo blue B in 50 ml. of ice water; this required vigorous shaking. The dye solution was kept in an ice bath until used. After incubation 0.2 ml. of 20% sodium carbonate solution was added to acid substrates. Then, 1 ml. of dye solution was added, with shaking, to each tube. Three minutes later 1 ml. of 40% trichloroacetic acid was added. To extract the diazo-coupled *beta*-naphthol, 10 ml. of ethyl acetate was added to each test tube. The tubes were shaken and centrifuged, and the absorbance of the ethyl acetate layer was determined at 540 mμ in a Beckman Model B spectrophotometer.

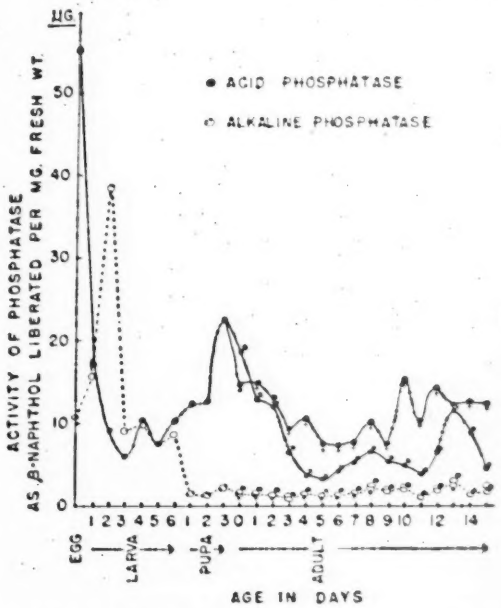


FIG. 1.—Average phosphatase activity in the brei of house flies of different ages. A sodium *beta*-naphthol-phosphate substrate was used.

RESULTS

The data on phosphatase activity are presented in figure 1.

[1]Accepted for publication December 7, 1957.
[2]The authors are indebted to Frank H. Babers for exploratory work on analytical methods and for synthesis of *beta*-naphthol phosphate.

TABLE I

BETA-NAPHTHOL LIBERATED FROM FLY BREI IN 1 HOUR AT 37° C. WITH A SUBSTRATE CONTAINING SODIUM BETA-NAPHTHOL PHOSPHATE

STAGE AND AGE (DAYS)	NUMBER OF TESTS	MICROGRAMS OF BETA-NAPHTHOL PER MG. OF BREI			
		Acid Phosphatase		Alkaline Phosphatase	
		Average	Range	Average	Range
Egg					
0	4	55 3	50 2-64 0	10 7	5 9-16 4
Larvae					
1	2	17 0	16 3-17 7	15 6	15 4-15 8
2	6	9 1	4 1-17 6	38 4	15 8-79 8
3	2	6 0	5 4- 6 7	9 0	8 4- 9 7
4	4	10 3	5 1-15 8	9 9	5 4-14 8
5	2	7 6	6 6- 8 5	7 6	7 5- 7 8
6	6	10 2	8 0-13 1	8 7	5 0-13 9
Pupae					
1	6	12 4	10 9-14 5	1 3	0 6- 2 0
2	6	12 8	10 2-18 2	1 1	0 8- 1 5
3	6	22 3	15 7-32 9	2 1	1 8- 2 3
Adult males					
0	6	18 8	15 8-24 8	1 8	1 7- 2 0
1	10	13 0	7 4-20 8	1 7	1 0- 2 9
2	10	12 0	7 3-15 1	1 2	0 2- 1 8
3	6	6 5	4 2- 8 3	0 8	0 2- 1 5
4	4	3 9	2 0- 6 8	1 4	1 3- 1 5
5	6	3 2	2 6- 5 0	1 2	0 6- 1 9
6	10	4 3	1 7- 8 3	1 2	0 6- 3 0
7	10	5 2	3 2- 9 8	1 7	1 0- 2 7
8	4	6 9	6 0- 7 7	2 8	2 2- 3 4
9	6	5 5	4 3- 7 0	1 8	1 0- 2 4
10	2	5 0	3 8- 6 3	2 0	1 9- 2 0
11	2	4 0	3 5- 4 4	1 0	1 0- 1 1
12	4	6 8	5 0- 8 9	1 9	1 0- 2 8
13	4	11 8	10 1-13 1	3 1	1 5- 4 9
14	2	9 0	8 2- 9 9	1 2	1 2- 1 2
15	2	4 6	4 2- 4 9	1 9	1 9- 1 9
Adult females					
0	6	14 7	10 2-19 9	1 3	1 1- 1 6
1	10	15 0	10 6-22 7	1 6	0 9- 2 0
2	10	13 1	10 3-17 6	1 6	1 1- 2 5
3	8	9 2	7 6-12 1	1 4	1 2- 1 8
4	4	10 7	9 8-12 3	1 9	1 6- 2 3
5	8	7 7	2 8-14 5	1 4	1 0- 2 2
6	10	7 4	5 5-10 2	1 3	0 4- 2 3
7	12	7 9	4 0-14 9	1 6	0 7- 3 2
8	8	10 2	6 2-15 2	2 1	1 5- 2 9
9	6	7 4	5 8- 9 4	2 0	1 9- 2 1
10	6	15 4	14 2-17 0	2 7	2 3- 3 1
11	4	10 1	7 9-11 8	1 2	1 0- 1 3
12	8	14 3	8 6-21 3	2 4	1 2- 3 3
13	6	12 1	8 2-21 3	2 6	1 1- 3 1
14	4	12 9	7 7-17 8	1 7	0 9- 2 5
15	6	12 6	8 9-17 1	2 7	2 6- 2 9
Larval medium					
0	4	9 6	7 3-12 9	0 6	0 4- 0 8
6	4	1 0	0 8- 1 5	0 4	0 4- 0 5

Acid phosphatase was most active in the egg stage. Two-day-old larvae had about 20% as much activity per milligram as eggs. This activity increased during the puparial stage and reached a maximum at about the time of adult emergence, but was not quite half as high as in the eggs. By the time adults were 3 days old the activity had decreased. Adult females had more acid phosphatase activity than males, except for newly emerged flies in which sex determination was difficult and uncertain.

The alkaline phosphatase activity built up to a high level in young larvae, but decreased to a low level by the time of puparium formation and remained low and almost constant throughout the adult stage. Alkaline phosphatase activity was the same in both sexes.

Results were most variable in eggs, young larvae, or pupae, in which the phosphatase activity changes rapidly with aging (Table 1). Conceivably, a more refined technique of sample selection which takes into account factors such as embryo stage, instars, or pupal structures may give more consistent results and amplify the observed changes.

Only the survivors were sampled. Males were scarce in cages of adults more than 9 days old. If a critical level of acid phosphatase activity determines survival, then this activity should approach a self-limiting constant in survivors as dead flies are eliminated with old age. Such a limit was not evident; the females always had more of this activity than the males. The longer life of the females therefore seems unrelated to their higher acid phosphatase activity.

Fly ovaries failed to develop on the sugar-water diet. Although no eggs were observed, a few females might have fed on dead flies or contaminants in the cages to obtain nutrients essential for egg production; such eggs, of course, could cause unusually high acid phosphatase activity in gravid females.

Further tests employing histochemical techniques are planned, which may indicate the sites of high acid phosphatase activity in eggs and late pupae and of alkaline phosphatase in 2-day-old larvae.

CONCLUSIONS

Acid phosphatase activity is higher in female than in male adult house flies and highest in eggs and in the contents of puparia. It seems to accompany tissue transformation.

Alkaline phosphatase activity is highest in 2-day-old larvae, and in adults was the same in both sexes.

Acid phosphatase activity does not seem to be self-limiting in surviving adults, and therefore did not imply an association with the increased longevity of females.

REFERENCES CITED

Alexander, B. H., R. J. Barker, and **F. H. Babers.** 1958. The phosphatase activity of susceptible and resistant house flies and German cockroaches. Jour. Econ. Ent. (in press.)

Chemical Specialties Manufacturers Association. 1955. Peet-Grady method. Soap and Sanit. Chem. Blue Book, pp. 249–50, 267.

Rockstein, M. 1956. Some biochemical aspects of aging in insects. Jour. Gerontol. 2: 282–5.

Seligman, A. R., H. H. Chauncey, M. M. Nachlas, L. H. Manheimer, and **H. A. Ravin.** 1951. The colorimetric determination of phosphatases in human serum. Jour. Biol. Chem. 190: 7–15.

THE USE OF ARTIFICIAL HEAT TO INDUCE MOSQUITOES TO FEED ON COLD-BLOODED ANIMALS[1]

EDWIN R. WILLIS

Pioneering Research Division, U. S. Army Quartermaster Research and Engineering Center, Natick, Massachusetts

ABSTRACT

During 10-minute tests, females of *Aëdes aegypti* and *Anopheles quadrimaculatus* accepted an artificially warmed frog (*Rana pipiens*) as a host, whereas they had ignored the frog when it was at room temperature; the difference in response was significant. *Aëdes aegypti* fed in significantly greater numbers on a warmed toad (*Bufo terrestris americanus*) than on the same animal when it was cold. *Anopheles quadrimaculatus* did not feed on the warmed toad. Neither species fed in significant numbers on a warmed lizard (*Phrynosoma cornutum*), although *Aëdes aegypti* was attracted by the warm animal.

Heat has been recognized as an attractant for mosquitoes for about 50 years (Rees, 1901; Howlett, 1910; Marchand, 1918; Crumb, 1922; van Thiel, 1937; Woke, 1937; Peterson and Brown, 1951; Laarman, 1955; Knierim *et al.*, 1955; and others). In the experiments below, three species of vertebrate poikilotherms were artificially warmed above the temperature of the surrounding air. Female mosquitoes were in-

[1]The experimental work on which this paper is based was completed in 1946 under a contract between the Office of the Quartermaster General, U. S. Army, and the Ohio State University Research Foundation.

Accepted for publication November 18, 1957.

duced to feed on two of the warmed hosts, whereas the same insects had been but little attracted by the cold animals. Modifications of the described technique may be useful in inducing feeding by mosquitoes on other relatively unattractive hosts.

MATERIAL AND METHODS

Two species of mosquitoes were used: *Aëdes aegypti* (L.) and *Anopheles quadrimaculatus* Say. They were 1 to 1½ weeks old when tested; all females in any one test were of the same age (within one day), and none had previously had a blood meal. From emergence until the day before the test, they were fed water and 5% honey solution. For 18–24 hours before the test, they were confined in a test cage (11 x 11 x 15 inches) and were allowed water only.

Three species of cold-blooded vertebrates[2] were used as hosts: the frog *Rana pipiens* Schreber, the toad *Bufo terrestris americanus* (Holbrook), and the horned lizard *Phrynosoma cornutum* (Harlan). The same host was offered both cold and warm to each species of mosquito. Because of their activity, the frog and toad were tied to boards with their legs extended; the lizard was not curbed.

Each test was divided into two phases. First, each host was offered to the mosquitoes at its normal body temperature for 10 minutes; then, after its temperature had been raised artificially, it was offered again to the same insects for a second 10-minute period. Host skin temperatures were measured before and after each phase of the test with a mercury-in-glass thermometer.

Heat was added to the frog and to the lizard when its skin was wet by immersing the animals in warm water for 10–15 minutes. The lizard was warmed with a dry skin in warm dry sand. The toad was warmed with an infrared heat lamp. Climatic conditions in the underground laboratory in which the tests were run remained relatively constant during the two phases of each test. The light intensity at the level of the host within the cage was 19 foot-candles.

TABLE I

RELATION BETWEEN SKIN TEMPERATURE OF *Rana pipiens* AND FEEDING BY MOSQUITOES DURING 10-MINUTE PERIODS

Test No.	Host Skin Temperature °F.		No. of ♀ Mosquitoes		Chi-Square[1]	P	Room Conditions	
	Start of Test	End of Test	In Cage	That Fed			R.H. %	Air Temp. °F.
Aëdes aegypti								
1a[2]	74°	74°	90	1			42	77°
1b[3]	94.5°	85°	89	15	184.6	< .001	42	77.5°
2a	74°	74°	85	0			42	78°
2b	95°	85°	85	18	275.5	< .001	42	78°
3a	75.5°	75.5°	92	0			43	78.5°
3b	94.5°	84.5°	92	4	6.32	< .02	43	78.5°
Anopheles quadrimaculatus								
4a	76°	76°	98	0			43	79°
4b	93°	84°	98	8	42.7	< .001	43	79°
5a	76.5°	76.5°	100	0			38	78°
5b	95°	85°	100	5	12.4	< .001	38	79°
6a	76°	76°	100	0			38	79°
6b	93°	83.5°	97	8	43.2	< .001	38	79°

[1]Calculated on the basis that at least one female might have been expected to feed in the control tests; deviations from expected ratios adjusted by Yates' correction for continuity (Snedecor, 1938).

[2]In all "a" tests, the host was presented to the mosquitoes at its normal temperature (control tests).

[3]In all "b" tests, the temperature of the host was raised artificially prior to start of test.

RESULTS

The numbers of both species of mosquitoes that fed on the warmed frog were significantly greater than the numbers that fed on the same host at its normal body temperature (Table I). Similarly, heat greatly enhanced the initial attractiveness of the toad to *Aëdes aegypti* (Table II); the numbers of this species that fed on the warmed toad were significantly greater than those that fed on the cold host. However, heat induced only one female of *Anopheles quadrimaculatus* to feed on the toad, although many probed the warm board to which the toad

[2]Dr. John W. Price, Department of Zoology and Entomology, Ohio State University, kindly identified the vertebrate species.

TABLE II

RELATION BETWEEN SKIN TEMPERATURE OF *Bufo terrestris americanus* AND FEEDING BY MOSQUITOES DURING 10-MINUTE PERIODS

Test No.	Host Skin Temperature °F.		No. of ♀ Mosquitoes		Chi-Square[1]	P	Room Air Temp. °F.
	Start of Test	End of Test	In Cage	That Fed			
Aedes aegypti							
7a[2]	75.5°	75.5°	95	12			78°
7b[3]	89°	78°	83	37	66.1	< .001	78°
8a	78°	78°	88	17			78°
8b	90°	79°	70	34	32.8	< .001	78°
Anopheles quadrimaculatus							
9a	74°	74°	44	0			77.5°
9b	91°	79.5°	44	0			77.5°
10a	78°	78°	99	0			78°
10b	87°	78°	98	0			78°
11a[4]	77°	77°	97	0			78°
11b[4]	91°	79°	97	1			78°

[1]Calculated with the ratios obtained in the control tests; deviations from expected ratios adjusted by Yates' correction for continuity (Snedecor, 1938).
[2]In all "a" tests, the host was presented to the mosquitoes at its normal temperature (control tests).
[3]In all "b" tests, the temperature of the host was raised artificially prior to start of test.
[4]A different toad was used for these tests.

TABLE III

RELATION BETWEEN SKIN TEMPERATURE OF *Phrynosoma cornutum* AND FEEDING BY MOSQUITOES DURING 10-MINUTE PERIODS

Test No.	Host Skin Temperature °F.		No. of ♀ Mosquitoes		Room Conditions		Condition of Host's Skin
	Start of Test	End of Test	In Cage	That Fed	R.H. %	Air Temp. °F.	
Aedes aegypti							
12a[1]	77°	77°	90	1	34	77°	Dry
12b[2]	94°	80°	89	1	34	77°	Dry
13a	77°	77°	80	1	36	77°	Wet
13b	94°	75.5°	79	1[3]	36	78°	Wet
14a	78°	78°	90	0	40	77°	Dry
14b	97°	82.5°	90	0	40	78°	Dry
15a	77.5°	77.5°	87	1	40	78°	Wet
15b	92°	77°	86	0	40	78.5°	Wet
Anopheles quadrimaculatus							
16a	76°	76°	90	0	33	76°	Dry
16b	94°	79°	90	0	33	76°	Dry
17a	75.5°	75.5°	85	0	36	77.5°	Wet
17b	95°	76°	85	0	36	78°	Wet

[1]In all "a" tests, the host was presented to the mosquitoes at its normal temperature (control tests).
[2]In all "b" tests, the temperature of the host was raised artificially prior to the start of test.
[3]A few mosquitoes landed on the lizard and probed briefly.

was tied; these same insects were quickly attracted to the human hand at the end of the tests, which showed that they were responsive to adequate stimuli.

In contrast to its response to the two amphibians, *Aëdes aegypti* did not readily feed on the heated lizard, either wet or dry (Table III). The heavily scaled skin of the lizard was an effective barrier that prevented most of the mosquitoes from feeding, even though they were attracted by the heat. More *Aëdes aegypti* landed and probed the warm lizard when its skin was wet than when it was dry; humidity apparently reinforced the heat stimulus. *Anopheles quadrimaculatus* did not respond to the lizard when it was offered either warm or cold.

Eggs were produced by mosquitoes of both species that had fed on frog blood; these eggs hatched and the larvae developed normally. Eggs laid by *Aëdes aegypti* that had fed on the toad also hatched. The single female of *Anopheles quadrimaculatus* that fed on toad blood died without ovipositing. Of the *Aëdes aegypti* that fed on the lizard, 1 was killed accidentally, 3 died within 24 hours after feeding, and the fifth died some time later without ovipositing.

DISCUSSION

Other workers have tried to feed mosquitoes on cold-blooded vertebrates with more or less success. In the experiments cited below, the temperatures of the hosts presumably differed little from the ambient temperatures, and the mosquitoes were attracted to the hosts by stimuli other than heat.

Nuttall and Shipley (1902) reported that *Anopheles maculipennis* would not feed on the toad *Bufo vulgaris*. Gordon (1922) could not induce *Aëdes aegypti* to bite the common wall gecko in Brazil. On the other hand, Woke (1937) found that during a 3-hour period 52% and 84%, respectively, of *Aëdes aegypti* fed on a frog (*Rana clamitans*) and a turtle (*Terrapene carolina*). Remington (1945) found the following amphibians readily acceptable hosts for *Uranotaenia lowii*: *Bufo valliceps*, *Bufo woodhousii fowleri*, *Rana sphenocephala*, *Hyla cinerea cinerea*, and *Desmognathus fuscus auriculatus*; but he also found that this mosquito showed no perceptible interest in the reptiles *Terrapene carolina*, *Anolis carolinensis*, and *Leicolopisma laterale*.

Unidentified mosquitoes have been seen feeding on small live fish which had surfaced (Murray, 1885; Combes, 1896). Murray watched mosquitoes kill over twenty fresh-hatched trout by inserting their proboscides into the fish's brains and sucking out the blood.

Although invertebrates have been seen acting as hosts for mosquitoes, experiments to confirm this have not been particularly successful. Nuttall and Shipley (1902) could not induce *Anopheles maculipennis* to feed on an earthworm. Remington (1945) exposed earthworms and shelled and shell-less, terrestrial Gastropoda to *Uranotaenia lowii*, but the mosquitoes did not feed. However, attacks on other insects by mosquitoes have been reported. Veazie (cited by Howard, 1901) observed Culicidae feeding on the pupa of *Cicada*. Hagen (cited by Howard, 1900) saw a mosquito feed on the chrysalis of a butterfly. Konokhov (1924) observed numbers of *Anopheles* feeding on *Cimex lectularius* and *Pediculus humanus* which were on mattresses placed in the sun for disinfection.

From the experiments reported herein, we would expect mosquitoes to start feeding sooner and to continue feeding longer on artificially heated hosts than on cold hosts. The heat lost to the surrounding air is the stimulus to which the host-seeking mosquitoes respond. Hence, if the heat gradient between the host and the air decreases, the heat stimulus will affect the mosquitoes less and less. Presumably, the phenomenon of decreasing stimulation with time reduced the numbers of mosquitoes that might have fed during 10-minute test periods. Heat loss from the warmed frog (weight 34g) and the warmed toad (weight 24g) was about 1°F. per minute. Heat loss from the warmed lizard (weight 12.8g) was at least 1.6°F. per minute and possibly more; the lizard's body temperature may have reached equilibrium with the surrounding air in less than 10 minutes and before the end of the test.

In future tests, an attempt should be made to hold the host animal at a constant temperature. Instead of preheating the host, as we did, an electric hot plate that could be maintained at a constant low temperature might be used to supply heat to the host throughout the test.

REFERENCES CITED

Combes, P. 1896. Les moustiques de l'isle d'Anticosti. Rev. Sci., Paris (4)6: 751–3.

Crumb, S. E. 1922. A mosquito attractant. Science 55: 446–7.

Gordon, R. M. 1922. Notes on the bionomics of *Stegomyia calopus* Meigen, in Brazil. Part II. Ann. Trop. Med. and Parasitol. 16(4): 425–39.

Howard, L. O. 1900. Notes on the mosquitoes of the United States. U. S. D. A., Div. Ent., Bull. No. 25, New Ser., 70 pp.

1901. Mosquitoes. New York: McClure, Phillips and Co., p. 34.

Howlett, F. M. 1910. The influence of temperature upon the biting of mosquitoes. Parasitology 3(4): 479–84.

Knierim, J. A., A. O. Lea, J. B. Dimond, and D. M. DeLong. 1955. Feeding adult mosquitoes on preserved blood to maintain egg production. Mosquito News 15(3): 176–9.

Konokhov, . 1924. [New biological peculiarities of *Anopheles*.] (In Russian.) Russ. Jour. Trop. Med., 1924(2): 48–49. [Rev. App. Ent. B12: 77(1924).]

Laarman, J. J. 1955. The host-seeking behaviour of the malaria mosquito *Anopheles maculipennis atroparvus*. Drukkerij en Uitgevers-Maatschappij v/h Kemink en Zoon N.V., Utrecht, 144 pp.

Marchand, W. 1918. First account of a thermotropism in *Anopheles punctipennis*, with bionomic observations. Psyche 25: 130–4.

Murray, C. H. 1885. [Quotation from Bulletin of U. S. Fish Commission.] Nature 32: 515.

Nuttall, G. H. F., and **A. E. Shipley.** 1902. Studies in relation to malaria. II. The structure and biology of *Anopheles*. Jour. Hygiene 2: 58–84.

Peterson, D. G., and **A. W. A. Brown.** 1951. Studies on the responses of the female *Aëdes* mosquito. Part III. The response of *Aëdes aegypti* (L.) to a warm body and its radiation. Bull. Ent. Res. 42: 535–41.

Rees, D. C. 1901. Malaria—its parasitology. The Practitioner, London, 66: 271–300.

Remington, C. 1945. The feeding habits of *Uranotaenia lowii* Theobald. (Diptera: Culicidae). Ent. News 56: 32–37, 64–68.

Snedecor, G. W. 1938. Statistical methods. Ames, Iowa: Collegiate Press, Inc., p. 169.

vanThiel, P. 1937. Quelles sont les excitations incitant l'*Anopheles maculipennis atroparvus* à visiter et à piquer l'homme ou le bétail? Bull. Soc. Path. Exot. 30: 193–203.

Woke, P. A. 1937. Cold-blooded vertebrates as hosts for *Aedes aegypti* Linn. Jour. Parasitol. 23(3): 310–11.

COMPARATIVE STUDY OF THIRTEEN SPECIES OF SARCOSAPROPHAGOUS CALLIPHORIDAE AND SARCOPHAGIDAE (DIPTERA)[1] I. BIONOMICS[2]

ADEL S. KAMAL

Department of Entomology, Colorado State University, Fort Collins

ABSTRACT

The species studied, representing nine genera in the two families, were: *Wohlfartia opaca* (Coq.), *Sarcophaga cooleyi* Park., *S. shermani* Park., *S. bullata* Park., *Protocalliphora avium* (S. & D.), *Phormia regina* (Meig.), *Protophormia terraenovae* (R. D.), *Phaenicia sericata* (Meig.), *Eucalliphora lilaea* (Walker), *Cynomyopsis cadaverina* (R. D.), *Calliphora vomitoria* (L.), *C. vicina* R. D., and *C. terraenovae* Macq. All except *W. opaca* and *P. avium* were reared successfully at 80 ±2° F. and 50±2 percent relative humidity; life history data on the other 11 species are tabulated and discussed. Controlled temperature and humidity, as employed here, accelerated the life cycle and shortened the adult life in comparison with results under fluctuating room temperature conditions. Beef liver was the most suitable rearing and oviposition medium. All species studied except *E. lilaea* avoided hog liver as a rearing medium, and all the calliphorids except *E. lilaea* (but none of the sarcophagids) required protein meal prior to copulation. Both protein and carbohydrates were required for oviposition. Severe competition for food prolonged the larval feeding period and gave rise to a large population of small-sized individuals; the sex ratio remained unaffected in underfed populations. Inherent ability to meet a critical shortage of food varies in different species; it is dependent upon whether the larvae has obtained the minimum food required to satisfy the physiological level of their metamorphosis and further their development. The possible significance of this inherent ability is in providing the mechanism of adaptation, which in turn influences distribution and population density of the species.

INTRODUCTION

Since the turn of the century, and mainly because of the great damage caused by blow flies to the sheep industry, a considerable number of workers have been engaged in the study of blow fly biology and distribution throughout the world (Lowne, 1890–95; Herms, 1907, 1928; Wardle, 1930; I. M. MacKerras, 1930; M. J. MacKerras, 1933; Tillyard and Seddon, 1933; Fuller, 1934; Hafez, 1940; and James, 1947). The taxonomic status and phylogenetic relationships of these flies have been covered by the excellent work of Aldrich (1916), Hall (1948), Roback (1954), and James (1955). The effects of temperature and humidity on their biological activities have been studied independently by several workers, including Evans (1934, 1935a, 1935b, 1936), Davies and Hobson (1935, 1937), Davidson (1944), Green (1951), and Ulyett (1955). The gross nutritional requirements were studied by Baumberger (1919), Michelbarger *et al.* (1932), and Hobson (1935a, 1935b, 1935c).

The findings of these investigators are major contributions to our present knowledge of this highly important group of flies. However, on the one hand these data lack universal agreement, and on the other they have left several problems unsolved. The present investigation is essentially an ecological study to determine the effect of controlled temperature and humidity on the life history, rate of development and other biological activity of both adults and immature stages of thirteen species of flies, representing nine genera within the families Sarcophagidae and Calliphoridae. Another portion of the investigation was devoted to the study of nutritional aspects of larval forms with special emphasis on how the quantity and quality of food affect life span, rate of growth, and the size of both the individual and the population.

MATERIALS AND METHODS

The present investigation was conducted in

[1]Portion of a dissertation presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology at The State College of Washington.

[2]Accepted for publication December 20, 1957.

the insectary of The State College of Washington from the fall of 1951 to the spring of 1956. In the summer of 1952 an air conditioning unit[3] was installed, and since that time controlled conditions were set at 80°±2° F. and 50±2 percent relative humidity. The rearing insectary was also provided with four ordinary light bulbs which burned continuously throughout the experiment.

Thirteen species representing nine genera within the families Sarcophagidae and Calliphoridae were studied. The sarcophagids include the following:

(1) *Wohlfahrtia opaca* (Coq.), probably a facultative subcutaneous furuncular parasite, but one which very readily and habitually adapts itself to a parasitic existence. The natural host is not known, but in the Pacific Northwest it infests young mink only three to four weeks of age, as well as the young of other mammals. Larval material was collected from mink ranches in the vicinity of Spokane, Washington. Adult flies for biological studies were collected from the vicinity of Pullman and Latah, Washington. (2) *Sarcophaga cooleyi* Park. (3) *Sarcophaga shermani* Park. (=*S. exuberans*, Rockstein and Kamal, not Pandelle). (4) *Sarcophaga bullata* Park. The above species of *Sarcophaga* are considered scavengers, but were reported by James (1947) to cause occasional myiasis in man and animals.

Among the calliphorids are the following species: (5) *Protocalliphora avium* (S. and D.) (=*Apaulina avium*, Rockstein and Kamal, not Pandelle), an obligate blood-sucking parasite of nestling wild birds reported as parasitizing crows and magpies (Jellison and Philips, 1933). The larval material for enzyme studies was collected from nestling magpies on May 27, 1951 from the vicinity of Moscow, Idaho. (6) *Phormia regina* (Meig.). (7) *Protophormia terrae-novae* (R. D.). (8) *Phaenicia sericata* (Meig.). (9) *Eucalliphora lilaea* (Walker). (10) *Cynomyopsis cadaverina* (R. D.). (11) *Calliphora vomitoria* (L.). (12) *Calliphora vicina* R. D. (13) *Calliphora terraenovae* Macq. All specimens were collected from the vicinity of Pullman, Washington.

All species, with the exception of *P. avium* and *W. opaca*, were reared in the insectary. Several attempts to rear *W. opaca* were unsuccessful. The adult flies throughout the entire investigation were maintained in screen cages (18″×18″×24″). A smaller size (12″×12″×18″) was used for comparative studies on the life span of the adult.

Beef liver, as the oviposition medium, was placed on petri dishes inside the cages. In all cages, except when indicated, the liver was not provided until copulation was first noticed, whereas sugar cubes and water were provided immediately after emergence. Water was made constantly available. Other media such as hog liver, kidney, ground beef, beef muscle, and dog biscuit (trade name—Friski) were used for rearing purposes. The relative suitability of these media as such is discussed later. When dog biscuits were used the cubes were crushed and soaked for thirty minutes.

Whenever oviposition (or larviposition in the case of sarcophagids) was noticed, the medium was removed from the cage and placed in a quart fruit jar two-thirds filled with medium size sawdust (90 to 100 grams) to which was added enough water (25 to 30 cc.) to wet the sawdust around the inside of the jar. The metal cap was replaced by a screen cap to permit ventilation. From three to six jars and from one to three cages were kept per generation.

For precise information on ovarian development, ovulation, copulation, and preoviposition period, pairs of equal and known age were placed separately under a glass lamp chimney, modified after Kamal (1954) and were observed very closely from two to four hours except from 1:00 a.m. to 8:00 a.m.

GENERAL BEHAVIOR

Feeding habits.—There is a definite difference in the feeding habits of the two families. It was observed that the sarcophagid larvae prefer natural openings as they make their entry into pieces of liver, which they ultimately leave with a leathery appearance, while the calliphorids try to make their own openings and usually leave the liver with a honey-combed appearance.

The three species of *Calliphora* and the *Cynomyopsis* caused a considerable staining of the sawdust with their waste products as they migrated downward. In all four species referred to above, a high mortality rate of the prepupal stage accompanied this penomenon and prepupae turned dark brown before death. Others which pupated failed to emerge and those which emerged produced deformed adults. Emergence rate for these species in question was the lowest. On the whole, the pupation medium of *Sarcophaga* was the least stained and odor was slight.

Response to light.—Several workers reported blow fly larvae to be negatively phototropic. Hall (1948) stated that the response becomes more marked with increasing age. In the present investigation, the newly hatched larvae remained close to their hatching site regardless of light for about 8 to 10 hours, but soon afterward they tended to avoid light for the rest of the larval period.

With the exception of the first year, this entire investigation was conducted under artificial light. No differences in reproductive capacity or mating activity were noticed whether rearing was under natural or artificial light.

Rearing media.—All species studied were reared on beef liver. However, some difficulty was encountered with *Calliphora* species. All species

[3]Hastings Air Conditioning Co., Inc., Hastings, Nebraska.

studied with the exception of *Phormia regina* and *Protophormia terrae-novae* oviposit readily on liver medium. These two species frequently avoided liver for oviposition purposes. Several batches of eggs were laid in the corners of the rearing cage and around the outside edges of the petri dish, but when these eggs were transferred to beef liver they developed normally and with no difficulty. One difficulty with liver as a rearing medium was that too small a piece tended to dry out rapidly and this in turn resulted in high egg mortality.

Some difficulty was encountered in stimulating oviposition on dog biscuit. The preoviposition period was extended when dog biscuit was first used, but it decreased gradually with succeeding generations until it leveled off. Females appeared to retain their eggs or larvae for more suitable media, but finally seem to give up.

When given a choice, all species, with the exception of *Calliphora* species, preferred beef liver over dog biscuit. Fresh beef liver proved more successful for bait and rearing. With the exception of *Eucalliphora lilaea*, all species showed a marked dislike for pork liver as a rearing medium, which they expressed by leaving the medium as early as the second instar and starting to wander around in sawdust. When forced to develop on pork liver, all instars, immatures as well as adults, were undersized. As an oviposition medium, however, the females were unable to distinguish it from beef liver.

Ground beef was tried as a rearing medium, but was later discarded in favor of beef liver. It has the disadvantage of drying out more rapidly than any other medium. Both ground beef and whole muscle were much more odoriferous than liver. On a few occasions, because of shortage of liver supply, larvae were reared on a mixture of liver and dog biscuits. Under such conditions, larvae seemed to survive very well, but did not invade dog biscuits until all the liver had been consumed.

Adult behavior.—In spite of the close similarities in life cycles and biologies of several species of Calliphoridae and Sarcophagidae, there are considerable variations in adult behavior and biological activities between members of the two families, taken collectively as well as among individual species within each family.

With the exception of *E. lilaea*, all calliphorids studied require a protein meal prior to copulation, but this is not necessary for the sarcophagids. Another difference is that all calliphorids studied, with no exception, deposit eggs, while sarcophagids usually deposit living larvae.

The adults of *Phormia regina* and *Protophormia terrae-novae* tended to congregate in the ceiling of the cages, often in the corners, and come down only for food and water. Their tendency to do so was more pronounced during the first week following emergence.

The adults of *Phaenicia sericata* are readily excited. When the cage was opened to care for flies, they became very agitated, flew rapidly, causing almost an uproar. Similar behavior, but to a much lesser degree, was exhibited by *Phormia regina*, *Protophormia terrae-novae*, and *Eucalliphora lilaea*. In the case of *Cynomyopsis cadaverina* and *Calliphora*, the flies were not at all disturbed when they were cared for and were very easy to catch.

On the other hand, the *Sarcophaga* species tended to play and box together. Very often within a week after emergence, the majority had broken wings. Often flies would tend to fall from the ceiling of the cage on the floor with a perceptible noise. Escaped flies in the insectary seldom showed such behavior. The relatively small size of the rearing cage seemed to contribute to this characteristic behavior, since most *Sarcophaga* are known to be strong fliers under natural conditions. In addition, the limited flying space of small cages shortened the life span of the adult *Sarcophaga*.

For the same number of individuals, the laboratory observations revealed that *Phaenicia sericata* consumed more sugar cubes than any other species studied. When the supply of sugar in the cage became exhausted for a period of 24 to 48 hours, over 75 percent of the flies died within the following 48 hours. In respect to their relative needs for sugar, the species studied fall in four groups as follows: Group I, *Phaenicia sericata*; group II, *Phormia regina*, *Protophormia terrae-novae*, and *Eucalliphora lilaea*; group III, *Cynomyopsis cadaverina*, and the *Calliphora* species; and group IV, *Sarcophaga cooleyi*, *S. shermani*, and *S. bullata*.

Among the calliphorids, mode of egg deposition varies from one species to another. *Eucalliphora lilaea*, *Phormia regina* and *Protophormia terrae-novae* were observed to discharge their eggs on the top of the bait in a cluster form. Clusters varied in size from 12 to 80 eggs each. Very often several clusters from various females were glued next to one another, often forming a heap of egg masses.

In the case of *Cynomyopsis cadaverina* and the genus *Calliphora*, eggs were usually laid singly and scattered on the top of the oviposition medium. In a few cases *Calliphora vomitoria* deposited its eggs on sugar cubes. On the other hand, the females of *Phaenicia sericata*, of all species studied, exhibited a distinct behavior. Eggs were deposited first in natural cavities and crevices of the liver. When such cavities were filled, females tended to discharge their eggs in moist spots under the surface of the bait. Usually one female deposited all the eggs which were ready for oviposition in a single cavity of the oviposition medium. Oviposition was more frequent following the introduction of fresh bait. The moist condition of the bait also accelerated oviposition.

The time required from depositing a batch of eggs varied not only from species to species, but with different individuals of the same species. In the case of *Eucalliphora lilaea*, it was recorded to require from 5 to 10 minutes, while *Phormia regina* and *Protophormia terrae-novae* required from 8 to 15 minutes. On the other hand, it was difficult to obtain a reliable estimate for species which deposit their eggs singly such as *Cynomyopsis cadaverina* and the *Calliphora* species. Members of these species visit the liver intermittently during oviposition.

The females of *Phaenicia sericata*, *Phormia regina*, *Protophormia terrae-novae*, and to a lesser degree *Eucalliphora lilaea* tended to leave the oviposition medium when flies were cared for. This is in contrast to *Cynomyopsis cadaverina* and the *Calliphora* species, which continue to deposit their eggs without paying any attention to such disturbance.

Lowne (1890) asserted that females of *Calliphora erythrocephala* controlled the number of her eggs to the available surface of oviposition medium. Such selective behavior does not occur in any of the species studied in the genus *Calliphora*, nor does it occur in *Phaenicia sericata*, *Phormia regina* or *Protophormia terrae-novae*. In these species females will continue to oviposit even though the available surface of oviposition medium is entirely covered with eggs.

If, after flies had been fed for a period of 5 to 7 days, the oviposition medium was removed from the rearing cages and kept from flies for periods of 0, 5, 10, and 15 days, the females appeared to retain their eggs until a suitable medium was provided. Oviposition was normal at 10- and 15-day intervals, but after this time, females were very erratic, oviposition becoming sporadic and the eggs produced being less viable. This retention of eggs within the females until a suitable medium was available may suggest a partial explanation of the viviparous habit of the Sarcophagidae. It might be worth mentioning in this regard that all the sarcophagids studied, unlike calliphorids, never larviposit on objects other than rearing media.

When ready to oviposit, the females examine the surface of the oviposition media apparently to find a suitable site. In doing so they usually behave in a certain pattern which varies from species to species. When a favorable spot is chosen, the females of *Eucalliphora lilaea*, *Phormia regina*, and *Protophormia terrae-novae* turn around in a circle a few times, often reversing direction and fluttering their wings, then protrude the ovipositor and the eggs are forced down.

Ovarioles studies.—Simple experiments were conducted in an attempt to obtain detailed information regarding development of ovarioles and egg production. Females were confined in the rearing cages with glass chimneys.

Confined females were dissected at one-day intervals following emergence to obtain information pertaining to the rate of egg development. In these studies, rearing media were provided from one to eight days following emergence. When time was not available for immediate examination, specimens were preserved in KAAD solution (Patterson, 1951) for subsequent examination. All dissecting and examining were performed with the aid of a dissecting microscope.

These dissections revealed that the time required under laboratory conditions for the first eggs to be completely developed was from 6 to 12 days. There was considerable variation in the degree of development from species to species and among different individuals of the same species. Age and the amount of food consumed by the female had a marked influence on individual variation. In the case of *Sarcophaga cooleyi*, the minimum time required for larval development within females was nine days from time of emergence. At this age, from 4 to 38 larvae per female were recorded. In comparison, there were from 26 to 54 larvae per female ten days following emergence. In both cases, flies were allowed only two days of feeding period starting on the fifth day following emergence. On the other hand, *Cynomyopsis cadaverina* females had from 76 to 168 eggs at the age of nine days. In comparison, there were at the age of ten days from 112 to 201, 121 to 243, and 87 to 178 for *Cynomyopsis cadaverina*, *Phaenicia sericata*, and *Eucalliphora lilaea*, respectively. In all cases and regardless of age, no eggs were developed prior to introduction of bait.

The undersized females which emerged from underfed larvae were examined and found, as one would expect, to have small ovaries and a reduced number of ovarioles, but were able to produce normal size eggs and adults.

IMMATURE STAGES

Life history.—The life history data have been treated in the sequence of their natural occurrence. The results presented in Table I demonstrate the marked differences among individual species as well as members of both families. Since the sarcophagids deposit living larvae, no data are available for egg development. Occasionally they laid eggs which appeared to be infertile, since none hatched, except that in a few instances batches of eggs deposited by *Sarcophaga shermani* and *S. cooleyi* hatched after a very short incubation period of approximately two hours and developed normally.

Eggs.—There is but little difference in the incubation periods of *Phormia regina*, *Protophormia terrae-novae*, and *Phaenicia sericata*. It took, on the average, 16 hours for the eggs to complete their development, but those of *Calliphora vicina*, *C. vomitoria*, and *C. terrae-novae* developed more slowly, leaving *Eucalliphora lilaea* and *Cynomyopsis cadaverina* to occupy an

intermediate position. Similarly there was but little difference in the percentage of egg hatchability among *Phormia regina*, *Protophormia terra-novae*, *Phaenicia sericata* and *Eucalliphora lilaea*. Under the same conditions all showed a high rate of egg survival and development compared with the three species of the genus *Calliphora*. *Cynomyopsis cadaverina* also occupied an intermediate position.

Larvae.—Overcrowding was avoided by adjusting the larval population to a given piece of rearing medium. It was observed that 125±5 grams of beef liver was sufficient to support normal growth of 125±5 calliphorid larvae and 100±5 sarcophagids. The morning after the larvae were introduced, the media were examined and either the excess of larvae was removed or additional food was provided.

registered by *Phormia regina* as 84 hours. In the same category lie *Protophormia terrae-novae*, *Phaenicia sericata*, *Eucalliphora lilaea* and *Cynomyopsis cadaverina*, with minor differences as shown in Table I. Those species were followed by *Sarcophaga shermani*, *S. cooleyi* and *S. bullata*, in that order. The species of the genus *Calliphora* constitute a distinct group by themselves. The longest prepupal period was recorded by *C. vomitoria* with a maximum of 504 hours. A high mortality rate of prepupae was recorded by all *Calliphora* species. No success was achieved in rearing any of the *Calliphora* species beyond the third generation. Data for the three species of *Calliphora* were obtained from two or more separate colonies.

Pupae.—The rate of pupal development lies approximately in the same order as that of the

TABLE I

LIFE HISTORY DATA OF 11 SPECIES OF SARCOSAPROPHAGOUS CALLIPHORIDAE AND SARCOPHAGIDAE REARED AT 80°±2° F. AND 50±2 PERCENT RELATIVE HUMIDITY

SPECIES	NO. OF GENERATIONS	EGG	FIRST STADIUM	SECOND STADIUM	THIRD STADIUM	PREPUPA	PUPA	TOTAL IMMATURE
		(Hrs.)	(Hrs.)	(Hrs.)	(Hrs.)	(Hrs.)	(Days)	(Days)
S. cooleyi	29		24(18-42)	18(9-30)	48(24-84)	96(42-144)	9(6-14)	16(14-18)
S. shermani	28		22(16-38)	16(8-24)	48(24-72)	104(30-168)	8(6-12)	14(12-16)
S. bullata	18		26(24-36)	18(14-24)	54(30-72)	112(54-192)	12(11-17)	17(16-20)
P. regina	23	16(10-22)	18(11-32)	11(8-22)	36(18-54)	84(40-108)	6(4- 9)	11(10-12)
P. terrae-novae	27	15(12-23)	17(12-30)	11(9-20)	34(20-60)	80(38-160)	6(4-10)	11(10-13)
P. sericata	29	18(12-38)	20(12-28)	12(9-26)	40(24-72)	90(48-192)	7(5-11)	12(12-15)
E. lilaea	27	22(14-30)	22(14-36)	14(9-24)	36(18-84)	92(54-204)	6(4-11)	13(12-16)
C. cadaverina	17	19(14-24)	20(16-30)	16(12-24)	72(36-96)	96(60-168)	9(7-12)	18(17-19)
C. vomitoria	5	26(23-29)	24(20-38)	48(43-54)	60(48-96)	360(240-504)	14(11-18)	23(21-27)
C. vicina	5	24(20-28)	24(18-34)	20(16-28)	48(30-68)	128(72-200)	11(9-15)	18(14-25)
C. terrae-novae	4	25(18-30)	28(26-36)	22(18-28)	44(30-58)	144(336-432)	12(10-17)	20(19-23)

*Duration of individual stadia given, as the mode, with the range expressed in parentheses.

The larval development involves essentially two molts and three stadia. There was a wide range of time required for each stadium as well as for each species studied. In considering the rapidity with which the larvae attained maximum growth, we find that *Phormia regina*, *Protophormia terra-novae*, *Phaenicia sericata* and *Eucalliphora lilaea* stand at the top of the list. These were followed by the genera *Calliphora*, *Sarcophaga* and *Cynomyopsis*, respectively. Within the genus *Calliphora* we find that *C. vomitoria* developed more slowly than *C. vicina* and *C. terrae-novae*. Similarly, *Sarcophaga bullata* developed more slowly than *S. cooleyi* and *S. shermani*.

Prepupae.—The prepupal stage is here defined as the wandering larva from the cessation of feeding to the beginning of the formation of the puparium. The shortest period for prepupal stage was recorded as 36 and 38 hours by few individuals of *Sarcophaga shermani* and *Protophormia terrae-novae*, respectively. On the other hand, the shortest mode for prepupal stage was

prepupae (Table I). It was found that the pupae of *Protophormia terrae-novae*, *Phormia regina*, and *Eucalliphora lilaea* developed most rapidly, with the other species arranged in the following order: *Phaenicia sericata*, *Sarcophaga shermani*, *Cynomyopsis cadaverina*, *Sarcophaga cooleyi*, *S. bullata*, and the three species of *Calliphora*. It will also be noticed that the total immature life span, from deposition of egg or larva to the emergence of the adult, varies from 11 days in *Phormia regina* to 23 days in *Calliphora vomitoria*.

ADULT STAGES

Life history data.—Table II summarizes the various biological aspects of adult stages of all species studied. The data represent a summary of 4 years' study, and except for *Sarcophaga bullata*, *Phormia regina*, and *Protophormia terrae-novae*, at least two colonies were reared simultaneously for each species studied.

Emergence.—A summary of emergence data is

presented in Table II. The emergence is expressed on a percentage basis as the ratio of the total number of puparia in at least two rearing jars selected at random from each generation.

The rate of emergence was found to be related to the moisture content of the sawdust. It was extremely hindered when no sawdust was provided, and considerably retarded in a completely dry sawdust.

Another factor which tended to extend the period of emergence was bacterial decomposition of the rearing media. This was especially true for all species studied in the genus *Calliphora* and to a lesser degree in *Cynomyopsis cadaverina*. This confirms the observation of MacKerras (1930). It was suggested that the slow-growing individuals find the medium less nutritive even though the amount of food is in excess of that needed.

In comparing the percentage and rate of emergence of the various species under consideration, it was found that the three species of *Calliphora* and *Cynomyopsis cadaverina* are the most susceptible to these variables (i.e., crowding, low humidity, etc.). On the other hand, *Eucalliphora lilaea*, *Phormia regina*, *Protophormia terrae-novae* and *Sarcophaga shermani* were the least affected. These were followed in order by *Phaenicia sericata*, *Sarcophaga cooleyi*, and *S. bullata*.

Copulation.—Copulation was recorded when noticed during the times that the flies were being cared for. It occurred in all cases from 2 to 9 days after emergence and it varies from species to species as shown by the data presented in Table II. Because of the relatively large population involving a dozen species, it was not possible to maintain a record for individual females. For these purposes, several tests using glass chimneys, as described previously, were employed. In case of sarcophagids, often a pair remained together for a couple of hours. The longest period of copulation recorded for a pair of *Sarcophaga cooleyi* was 3 hours 15 minutes. On the other hand, copulation among the calliphorids was very difficult to detect because of its short duration which seldom lasted more than a few minutes. In addition, especially *Phaenicia sericata*, *Phormia regina*, and *Protophormia terrae-novae* were very easily agitated, causing pairs in copula to separate.

Period of mating activity.—This period is expressed by the total number of days during which copulation was observed. The data presented in Table II showed *Phormia regina*, *Protophormia terrae-novae*, *Phaenicia sericata*, and *Eucalliphora lilaea* to exhibit the longest mating activity. No conclusive record for the three species of *Calliphora* is available.

TABLE II

LIFE HISTORY DATA OF 11 SPECIES OF SARCOSAPROPHAGOUS CALLIPHORIDAE AND SARCOPHAGIDAE REARED AT 80°±2° F. AND 50±2 PERCENT RELATIVE HUMIDITY[a]

SPECIES	NO. OF GENERATIONS	EMERGENCE PERCENT	EMERGENCE TO FIRST COPULATION	EMERGENCE TO FIRST OVIPOSITION OR LARVIPOSITION	OVIPOSITION OR LARVIPOSITION PERIOD	MATING ACTIVITY	ADULT LIFE SPAN
S. cooleyi	29	74–91	4–9	7–12	12(5–22)	13(5–20)	22(19–34)
S. shermani	28	81–93	4–8	7–11	17(6–21)	11(6–16)	26(17–31)
S. bullata	18	64–87	5–7	8–11	13(6–20)	7(5–11)	24(22–28)
P. regina	23	87–94	3–7	5– 8	22(18–28)	19(10–25)	52(45–68)
P. terra-novae	27	80–92	3–7	5– 9	27(16–34)	17(11–22)	55(48–71)
P. sericata	29	69–91	3–8	5–14	20(15–29)	15(9–19)	46(40–59)
E. lilaea	27	88–95	2–6	5– 9	14(9–15)	14(6–17)	23(18–41)
C. cadaverina	17	35–78	4–7	6–12	13(11–20)	9(6–14)	33(21–39)
C. vomiteria	5	42–68	4–8	7–18	10(5–14)		26(27–36)
C. vicina	5	31–43	5–9	8–15	6(2–15)		25(24–35)
C. terrae-novae	4	37–54	4–9	7–16	7(3–11)		27(29–38)

[a]Duration of each period is expressed in days as the mode, with the range in parentheses.

Preoviposition period.—The preoviposition period for several calliphorids has been reported under natural conditions by several workers. According to Lowne (1890–1895) the preoviposition period of *Calliphora vicina* lasts as long as four weeks. On the other hand, Bishopp (1915), reported the preoviposition period for *Phormia regina* to vary from 7 to 17 days. Under the controlled conditions employed here, the preoviposition period ranged from 5 to 18 days according to species. As shown in Table II, *Phormia regina*, *Protophormia terrae-novae*, *Phaenicia sericata* and *Eucalliphora lilaea* deposit eggs 5 days from emergence. The longest preoviposition period was recorded for the genus *Calliphora* with a maximum of 18 days in the case of *C. vomitoria*.

Oviposition period.—The data presented in Table II show the wide range over which ovi-

position period extends among different species. The longest period was recorded for *Protophormia terrae-novae* with 34 days. In the same neighborhood lie *Phormia regina* and *Phaenicia sericata*. These are followed by the genera *Sarcophaga* and *Cynomyopsis*.

Adult longevity.—The longevity under natural conditions is not known exactly. Salt (1932) reported a *Phaenicia sericata* to have lived 104 days in captivity. However, he recorded the average life span of *P. sericata* to be 56.6 days for females and 41 days for males. The data obtained from the present studies show considerable variation at different temperatures, and from one species to the next. The controlled temperature of 80° ±2° F. and relative humidity of 50±2 percent, as used here, tended to shorten the life span of the adult, as compared with those flies reared under fluctuating conditions. This was illustrated by the fact that the maximum life span under fluctuating conditions was recorded as 71, 69, 59, 41, and 34 days, as compared to 61, 63, 50, 29, and 25 days under controlled conditions for *Protophormia terra-novae*, *Phormia regina*, *Phaenicia sericata*, *Eucalliphora lilaea*, and *Sarcophaga cooleyi* respectively. The size of the rearing cages also influenced longevity. The larger the cage the longer the life span of the adult, especially in the Sarcophagidae.

INTRASPECIFIC COMPETITION AND ITS EFFECTS

The effect of competition for food among the individual members of a given species has been shown to produce a marked influence on the rate of growth, the size of the various developmental stages, the emergence and fecundity of the adult.

Effect on larval growth.—To study the effect of insufficient food supply, a crowded condition was induced in the laboratory by gradually increasing the larval population for a given piece of rearing medium. As crowded conditions reached a point where the available food became insufficient to support normal growth for all larval population, the larvae in excess were forced out of the rearing media and started to wander in the sawdust. If additional food was later provided, the larvae returned and resumed feeding. The active larval feeding period was thus extended. On the other hand, if no additional food was provided, the underfed larvae kept on migrating aimlessly in the sawdust, and finally shriveled and died. It was observed that the percentage of mortality is dependent upon whether the larvae had obtained the minimum food requirements to satisfy the physiological level of their metamorphosis and further their successful development. In many instances, mortality reached 80 precent under extremely crowded conditions.

Effect on pupae.—The shortage of food supply produced no significant effect on the rate of pupal development. Time required for pupal development under crowded conditions was very similar to that under normal conditions. The only marked effect was the reduction of size of the puparium which in turn produced an imago of reduced size. High pupal mortality was recorded under severe competition.

Effect on emergence.—Severe competition for food was associated with high pupal mortality and low rate of emergence. In addition, it was noticed that no peak of emergence was reached, but rather the emerging population was extended evenly for approximately 2 weeks as compared to a period of 3 to 6 days under normal conditions.

Effect on fecundity.—MacKerras (1933) reported that the fecundity of the fly depends upon its size, which in turn is dependent upon the amount of food consumed during the larval stage. This phase of the problem was further studied on quantitative bases by Ullyett (1950) and more recently by Webber (1955). The finding of the present investigation confirms the data of these workers, and in addition it revealed that the oviposition period was shortened in the underfed population as compared with the normal population.

Effect on sex ratio.—The emerging population from underfed larvae were counted and analyzed. No effect was noticed on sex ratio as reported by Herms (1928), either from competition or from shortage of food.

EFFECTS OF INADEQUATE DIET

Effect on fecundity.—Uvarov (1928) was among the early workers to observe that a protein diet was, in general, essential for reproduction and development of eggs in insects. On the other hand, Glaser (1923) reported *Musca domestica*, contrary to *Phormia regina*, as having produced a few eggs when reared on sucrose solution alone. Hobson (1938) working with *Lucilia* (= *Phaenicia*) *sericata* found that neither milk nor blood serum were effective in supporting egg development, whereas Dorman *et al.* (1938) found that *Phormia regina* developed eggs very well on milk. More recently Rasso and Fraenkel (1954) demonstrated that *Phormia regina* (Meig.) produces no eggs when fed only on protein diet that lacks carbohydrates.

Because of the variation in these results, several experiments were conducted to investigate the effect of inadequate diets on egg production in all species under consideration. For this purpose each experiment consisted of five replicates and each replicate consisted of 100 to 125 flies of each species studied. Flies were reared separately on various diets as follows: water alone, sugar alone, water and sugar, water and liver, and on all three substances. In all cases, no eggs were deposited when flies were reared on either sugar or liver alone. In the former, however, the ovaries remained undeveloped, while the ovaries of flies fed on liver superficially appeared to develop normally. Both sugar and liver were essential for oviposition.

Effect on adult longevity.—Graham-Smith

(1916), studying the effect of climate on populations of adult blow flies, reported a high death rate among newly emerged flies in nature. Recently Rasso and Fraenkel (1954) stated that in the absence of a carbohydrate diet, *Phormia regina* lived for a maximum of 6 days.

In an attempt to determine the effects of inadequate diets upon adult longevity, several experiments were conducted where, for each test, 100 to 125 flies of approximately equal sex ratio were released upon emergence into a cage and were immediately provided with the test diets which were as follows: water, sugar, water and sugar, and finally, water, sugar and liver as a normal diet.

Table III summarizes the adult life span of the various species studied under each separate diet.

TABLE III

MAXIMUM ADULT LONGEVITY[a] UNDER VARIOUS DIETS, 1951-55

SPECIES	WATER	SUGAR	WATER AND SUGAR	WATER, SUGAR AND LIVER
S. cooleyi	17	6	21	34
S. shermani	16	6	21	31
S. bullata	15	6	22	30
P. regina	7	10	22	69
P. terrae-novae	7	9	23	71
P. sericata	6	5	15	59
E. lilaea	6	6	19	41
C. cadaverina	8	6	20	39
C. vomitoria	8	5	21	36

[a]Expressed in days.

In general the sarcophagids lived considerably longer on water alone than they did on sugar alone, and as a whole, the calliphorids were generally more sensitive to lack of sugar than the sarcophagids. When reared on water alone, all calliphorids died more rapidly than the sarcophagids. In the case of *Phaenicia sericata* and *Eucalliphora lilaea*, both water and sugar were equally critical for adult longevity where approximately 75 percent of the flies were dead at the end of the fourth day after emergence. On the other hand, *Phormia regina* and *Protophormia terrae-novae* lived slightly longer on sugar than on water.

One other significant point was that the combined water and sugar diet not only increased longevity in all species studied, but the mortality rate was evenly distributed over the entire life span. When flies were reared on either sugar or water alone, death occurred in peaks. For example, approximately 50 percent of the Calliphoridae, when reared on sugar alone, were dead by the end of the third day, and from 75 to 95 percent (according to species) were dead after 4 days.

Similar mortality peaks were recorded for flies reared on water alone. But in this case peaks were extended over a somewhat wider range, and only in the case of *Protophormia terrae-novae*, *Cynomyopsis cadaverina*, and *Sarcophaga bullata* did a few individuals live up to 12, 13, and 20 days respectively.

DISCUSSION

Ullyett (1950) reported that food deficiency neither shortened nor lengthened the total growing period of the larvae, but rather resulted in "slowing up the growth increments during the period of most rapid growth." The data of this investigation showed that a critical shortage of food increased the duration of the larval period.

Various workers disagree as to the effect of intraspecific competition on pupal development. Fuller (1934) reported that no correlation exists between pupal development and intraspecific competition. On the other hand, Ullyett (1950) has found that undernourished larvae form puparia and pupate, yet they may die before transformation into adult flies. The findings of this study is in agreement with the observations of Ullyett.

The minimum size which larvae have to attain in order to pupate was found to vary from one species to another, and with different individuals within a given species. As the number of indidivudals in a given population increases while the food supply remains constant, the size of the developing individuals decreases to a point beyond which the resultant larvae fail to pupate. Under extreme crowding and severe competition, larval mortality increased up to 70 percent and the resultant pupae often failed to produce adults.

Eucalliphora lilaea, *Phormia regina*, *Protophormia terrae-novae* and *Phaenicia sericata* have shown more adaptability, especially as larvae, than any of the other species studied. They can better tolerate food deficiency, crowding, and low humidity. Most significant, probably, is the fact that they develop most rapidly, their immature stages being completed on an average of from 11 to 13 days. These species were followed in order by *Cynomyopsis cadaverina* and the three species of *Calliphora*. In the case of the sarcophagids, *Sarcophaga shermani* has shown more tolerance to crowding and food shortage than either *S. cooleyi* or *S. bullata*.

Because of its smaller size, *Eucalliphora lilaea* was observed to react more favorably to an increase in larval population than any of the other species studied. It is an extremely common species in eastern Washington. It breeds commonly in small carcasses, such as rodents and small birds. According to James (1947) it has never been reported in myiasis. On the other hand, the other three widely adapted species, *Phaenicia sericata*, *Phormia regina*, and *Proto-*

phormia terrae-novae, along with *Callitroga macellaria* (F.) are the most important producers of facultative myiasis in the United States. The fact that *Eucalliphora lilaea* is a small-carcass feeder gives it another advantage over the other species studied. This feature is of importance under natural conditions when several species are competing for limited amounts of food. A small carcass can support more individuals of *E. lilaea* on the basis of size than would be possible for other species.

Reduction in size, up to a point, constitutes an advantageous adaptation on the part of the individual and permits a larger population to develop from a given amount of food than would otherwise occur under normal conditions.

The above findings suggest probable reasons for the abundance of *Eucalliphora lilaea*, *Phormia regina*, *Protophormia terrae-novae* and *Phaenicia sericata*; all can better tolerate crowding, food shortage, and low humidity. Although other factors may enter into the picture under natural conditions, the fact remains that food supply within the limits of favorable environmental conditions plays a major role in determining the size of both the individual and the population.

Of all species studied, *Eucalliphora lilaea* under crowded conditions attains the smallest size of both larvae and adults, though under natural conditions some *E. lilaea* may be almost as large as the *Calliphora* species. The food requirement is proportional to the larval size.

Phormia regina, and to a lesser degree *Protophormia terrae-novae*, hold an advantage over all other species studied in that they attain their maximum growth in the least amount of time. Both species have the greatest period of mating activity and the longest life span. These features are important under natural conditions when several species are competing for limited amounts of food. Such biological characteristics appear to play a significant role in population density especially under unfavorable environmental conditions.

The high egg mortality among the three species of *Calliphora* in comparison with other calliphorids may be attributed to the slower rate of development of their eggs and the consequent death from desiccation. This is substantiated by Evans (1936) who reported the percentage of egg survival of the closely related species *Calliphora erythrocephala* at 25° C. and 80, 60, and 40 percent relative humidities to be 98 percent, 76 percent and zero, respectively. This may suggest one means by which *Eucalliphora lilaea* can better tolerate low humidity, since *E. lilaea* has practically the same incubation period as that of *Calliphora* species and yet has a much higher rate of egg survival.

Of all the species studied, *Phaenicia sericata* is the most intolerant of low humidity. Egg development was considerably reduced at 35 percent relative humidity and completely stopped at 25 percent. These findings are in agreement with those of Davies (1948), who indicated that the eggs of *Lucilia* (= *Phaenicia*) *sericata* are very sensitive to drying.

SUMMARY

1. Life history data of 11 species (all except *Wohlfahrtia opaca* and *Protocalliphora avium*) which were reared successfully at 80°±2° F. and 50±2 percent relative humidity are tabulated and discussed. No success, however, was achieved in rearing any of the *Calliphora* species beyond the third generation.

2. No differences in reproductive capacity or mating activity were noticed when rearing was under natural or artificial light.

3. Controlled temperature and humidity as employed here, speeded up the life cycle and shortened the adult life span in comparison with fluctuating conditions of room temperature.

4. The size of the rearing cages influenced the life span of the adult; the smaller the cage, the shorter the life span.

5. Beef liver was the most suitable medium for rearing and for oviposition. With the exception of *Eucalliphora lilaea*, all species studied avoided hog liver as a rearing medium. Fresh and moist liver proved more satisfactory for oviposition than old liver. Occasionally, *Phormia regina* and *Protophormia terrae-novae* deposited their eggs on objects other than rearing medium.

6. Some difficulty was encountered in stimulating oviposition on dog biscuit. Consequently, the preoviposition period was extended when dog biscuit was first used, but it decreased gradually with succeeding generations until it leveled off.

7. It required from 6 to 12 days from time of emergence for the first eggs to be completely developed. There were considerable variations from one species to another and among different individuals of the same species. Age and amount of food consumed by the female have a marked influence on individual variation.

8. With the exception of *Eucalliphora lilaea*, all calliphorids studied here required protein meal prior to copulation. This is not necessary in the case of sarcophagids. In respect to their relative need for sugar, the calliphorids were more susceptible to lack of sugar than the sarcophagids. When reared on water alone, all calliphorids died more rapidly than the sarcophagids. The sarcophagids lived considerably longer on water alone than they did on sugar. Both protein and carbohydrates were required for oviposition.

9. Severe competition for food prolonged the larval feeding period but had no effect on the pupation period.

10. Critical shortage of larval food supply gave rise to a large population with small sized individuals. The undersized individuals produced normal but comparatively fewer eggs.

This decrease in fecundity caused little competition among members of the resulting progeny which in turn produced normal sized individuals.

11. Sex ratio remained unaffected in underfed populations.

12. For a given set of environmental conditions (such as those used here), the avilability of food supply was the major factor limiting both the size of the individual and the population.

13. The inherent ability of a given species to meet the critical shortage of food supply varied from one species to the next and was dependent upon whether the larvae had obtained the minimum food requirements to satisfy the physiological level of their metamorphosis and further their successful development. The possible significance of this inherent ability is in providing the mechanism with which a given species can meet and adapt itself to the constant environmental changes and which in turn influences distribution and population density of the species.

ACKNOWLEDGMENT

The author is gratefully indebted to Dr. Maurice T. James, under whose direction this investigation was conducted, for his invaluable advice, warm encouragement, helpful suggestions, and critical reading of the manuscript, and to Richard B. Spurrier, whose investigations furnished part of the background material.

This investigation was supported in part by fund provided for Biological and Medical Research by The State College of Washington Initiative Measure 171.

REFERENCES CITED

Aldrich, J. M. 1916. *Sarcophaga* and allies in North America. 302 pages. Thomas Say Foundation, Lafayette, Indiana.

Baumberger, J. P. 1919. A nutritional study of insects, with special references to the microorganisms and their substrata. Jour. Exptl. Zool. 28: 1–81.

Bishopp, F. C. 1915. Flies which cause myiasis in man and animals—some aspects of the problem. Jour. Econ. Ent. 8: 317–29.

Davidson, J. 1944. On the relationship between temperature and rate of development of insects at constant temperatures. Jour. Animal Ecol. 8: 26–38.

Davies, L. 1948. Laboratory studies on the egg of the blowfly *Lucilia sericata* (Mg.). Jour. Exptl. Biol. 25: 71–85.

Davies, W. M., and **R. P. Hobson.** 1935. Sheep blowfly investigations. I. The relationship of humidity to blowfly attack. Ann. Appl. Biol. 22: 279–93.

1937. Sheep blowfly investigations. Jour. Minist. Agric. (London) 44: 222–30.

Dorman, S. C., W. C. Hale, and **W. M. Hoskins.** 1938. The laboratory rearing of flesh flies and relations between temperature, diet, and egg production. Jour. Econ. Ent. 31: 44–51.

Evans, A. C. 1934. Studies on the influence of the environment on the sheep blowfly, *Lucilia sericata* Meig. I. The influence of temperature and humidity on the egg. Parasitology 26: 366–77.

1935a. Studies on the influence of the environment on the sheep blow-fly, *Lucilia sericata* Meig. II. The influences of humidity and temperature on prepupae and pupae. Parasitology 27: 291–98.

1935b. Studies on the effect of the environment on the sheep blow-fly, *Lucilia sericata* Meig. III. The influence of humidity and temperature on the adult. Parasitology 27: 299–308.

1936. Studies on the effect of the environment on the sheep blow-fly, *Lucilia sericata* Meig. IV. The indirect effect of temperature and humidity acting through certain competing species of blow-flies. Parasitology 28: 431–39.

Fuller, M. E. 1934. The insect inhabitants of carrion: a study in animal ecology. Australia. Council Sci. and Indust. Res., Bull. 82. 62 pages.

Glaser, R. W. 1923. The effect of food on longevity and reproduction in flies. Jour. Exptl. Zool. 38: 383–412.

Graham-Smith, G. S. 1916. Observations on the habits and parasites of common flies. Parasitology 8: 440–544.

Green, A. A. 1951. The control of blowflies infesting slaughter houses. I. Field observations on the habits of blowflies. Ann. Appl. Biol. 38: 475–94.

Hafez, M. 1940. A study of the morphology and life history of *Sarcophaga falculata* Pand. (Diptera: Sarcophagidae). Bull. Soc. Fouad 1er Ent. 24: 183–212.

Hall, David G. 1948. The blow flies of North America. 477 pages. Thomas Say Foundation, Lafayette, Indiana.

Herms, W. B. 1907. An ecological and experimental study of Sarcophagidae with relation to lake beach debris. Jour. Exptl. Zool. 4: 45–83.

1928. The effect of different quantities of food during the larval period on the sex ratio and size of *Lucilia sericata* Meigen and *Theobaldia incidens* (Thom.). Jour. Econ. Ent. 21: 720–29.

Hobson, R. P. 1935a. Growth of blow-fly larvae on blood and serum. II. Growth in association with bacteria. Biochem. Jour. 29: 1286–91.

1935b. On a fat-soluble growth factor required by blow-fly larvae. I. Distribution and properties. Biochem. Jour. 29: 1292–6.

1935c. On a fat-soluble growth factor required by blow-fly larvae. II. Identity of the growth factor with cholesterol. Biochem Jour. 29: 2023–6.

1938. Sheep blow-fly investigations. VII. Observations on the development of eggs and oviposition in the sheep blow-fly, *Lucilia sericata* Mg. Ann. Appl. Biol. 25: 573–82.

James, M. T. 1947. The flies that cause myiasis in man. U. S. Dept. Agric. Misc. Publ. 631. 175 pages.

1955. The blow flies of California (Diptera: Calliphoridae). Bull. California Insect Surv. 4: 1–34.

Kamal, A. S. 1954. Ecological and nutritional studies on the cherry fruit fly. Jour. Econ. Ent. 47: 959–65.

Lowne, B. T. 1890–95. The anatomy, physiology, morphology and development of the blowfly. 2 volumes. R. H. Porter, London.

MacKerras, I. M. 1930. Recent developments in blowfly research. Australia. Council Sci. and Indust. Res., Jour. 4: 212–19.

MacKerras, M. J. 1933. Observations on the life histories, nutritional requirements and fecundity of blow-flies. Bull. Ent. Res. 24: 353–62.

Michelbacher, A. E., W. M. Hoskins, and **W. B. Herms.** 1932. The nutrition of flesh fly larvae, *Lucilia sericata* (Meig.). I. The adequacy of sterile synthetic diets. Jour. Exptl. Zool. 64: 109–32.

Rasso, S. C., and **G. Fraenkel.** 1954. The food requirements of the adult female blow fly, *Phormia regina* (Meig.), in relation to ovarian development. Ann. Ent. Soc. America 47: 636–45.

Roback, S. S. 1954. Evolution and taxonomy of Sarcophaginae (Diptera, Sarcophagidae). Illinois Biol. Mongr. 23(3–4): 1–181.

Salt, G. 1932. The natural control of the sheep blow fly, *Lucilia sericata* Meigen. Bull. Ent. Res. 23: 235–45.

Tillyard, R. J., and **H. R. Seddon** (ed.). 1933. The sheep blowfly problem in Australia. Australia. Council. Sci. and Indust. Res., Phamphlet 37. 136 pages.

Ullyett, G. C. 1950. Competition for food and allied phenomena in sheep blowfly populations. Phil. Trans. Roy. Soc. London B 234: 77–174.

Uvarov, B. P. 1928. Insect nutrition and metabolism. Trans. Roy. Ent. Soc. London 76: 255–343.

Wardle, R. A. 1930. Significant variables in the blow fly environment. Ann. Appl. Biol. 17: 554–74.

Webber, L. G. 1955. The relationship between larval and adult size of the Australian sheep blowfly, *Lucilia caprina* (Wied.). Australian Jour. Zool. 3: 346–53.

BEHAVIOR OF THE IMAGO OF THE CORN EARWORM, HELIOTHIS ZEA (BODDIE), WITH SPECIAL REFERENCE TO EMERGENCE AND REPRODUCTION[1]

PHILIP S. CALLAHAN[2]

ABSTRACT

The emergence and wing expansion of the imago is described. A villous surface from which the imago could hang was necessary for proper expansion and drying of the wings. 94.6 per cent of emergence occurred between 7:00 P.M. and 11:00 P.M. At a constant intensity of light below 0.89 foot-candles the imago remained active throughout the night. Activity is dependent upon stimulation for a short period of time by low intensity light rather than dependent upon some internal rhythm. Reproductive behavior is described and exposure of the abdomen by females was found to be important for successful copulation. Copulation took place on a lighted oviposition surface with females mating once in the cage and males up to three times. 56% of the females copulated. Length of life of mated females that died natural deaths had no effect on the number of eggs laid. Mated imagos lived longer than unmated imagos but imagos held inactive lived the longest. Length of life apparently depended on activity. Oviposition by mated moths always began on the second complete night after emergence. Oviposition as an active process is described. Infertile eggs are not oviposited but rather deposited as a process of squeezing out a few mature unfertilized eggs. Oviposition is continuous throughout the night with slightly greater oviposition from 7:30 P.M. to 1:30 A.M. The percentage of mated females from a field population was 36% compared to 56% for the caged population; however, the number of matings as determined by spermatophore counts was 57% for the field population, as many had mated more than once. Most of the mated field moths were middle aged and there was an increase in the percentage of mating as the night temperature increased. A list of food plants at which the imago feeds indicates that a great variety of different colored flowers in many different ecological environments are visited.

The results described in this paper are a portion of a more comprehensive dissertation on environmental factors affecting reproductive and oviposition behavior of the corn earworm moth. Observations, with the exception of those on the process of emergence and wing expansion, were made in a special behavior cage 18″ by 18″ by 30″. This cage, described in detail in another paper (Callahan 1957b), was constructed so that colored lights could be projected on cloth oviposition surfaces at either end. The intensity of light in the cage was below 0.89 foot-candles during all observations.

[1]Portion of a dissertation submitted in partial fulfillment of the requirements for the degree Doctor of Philosophy in Entomology, Kansas State College, 1956. Contribution No. 701, Department of Entomology, Kansas Agricultural Experiment Station, Manhattan. Acknowledgment is made to Dr. Reginald H. Painter for his advice on certain aspects of this study. Accepted for publication January 4, 1958.

[2]Assistant Professor, Entomology Research Department, Louisiana State University, Baton Rouge. Formerly Graduate Research Assistant in Entomology at Kansas State College, Manhattan.

BEHAVIOR OF THE IMAGO AT EMERGENCE

Shortly preceding emergence of the imago, the pupae became very active and rapidly rotated their bodies by means of arc-like twists of their abdominal segments. A few moments after the activity subsided the pupal cases split along the median dorsal line of the thorax and the imagos worked forward until free of the pupal case (Fig. 1, A). The chronological sequence of events which preceded the expansion of wings to their normal size and position varied but slightly among five moths which emerged at a temperature of 80° F. and upon which this description of emergence is based.

For a period of about 2 minutes after emergence the imagos became very active and crawled around as if in search of a surface from which to hang during wing expansion. The wings at this stage appeared as small oval pads approximately 6 mm. in length. Unless disturbed, the imagos quickly settled down in a hanging position on the under side of a suitable surface (Fig. 1, B). In this case, cotton percale was placed on one side

and across the top of the emergence jar to provide a villous surface to which the imagos could cling. The importance of such a surface was illustrated by the fact that pupae allowed to emerge in glass jars and provided with no surface other than the glass usually matured with crumpled, deformed wings. No deformed imagos were ever obtained from the jars provided with cloth. Only rarely did an imago cling to the side cloth in a vertical position rather than to the top cloth in a hanging position. The imagos maintain this typical hanging position, with the legs hooked into the cloth surface and the abdomen pointed downwards and arched dorsally, for an average period of 43 minutes. Of this total time during which the imago was hanging, 17 to 18 minutes passed before any change was noticeable in the wing pads (Fig. 1, B). After 17 minutes, a slight raised hump was observed in the center of each wing pad. This hump slowly enlarged for a period of 7 minutes (Fig. 1, C). As the hump expands the wings are gradually lengthened and the edges appear to bend under slightly. In approximately 6 minutes of the elapsed time, the whole wing surface appeared as a convex bowl. During the seventh minute the wings began to flatten out slightly, and at this point they were suddenly snapped over the back of the thorax and held tightly together against each other. They were maintained in this rigid, vertical position for the remaining 19 minutes (Fig. 1, D), after which they were suddenly snapped down to the normal, horizontal resting position. After a short rest the imagos again became active. Generally the imagos explored the cage until a good position was found on a vertical surface; they then pumped their wings up and down and ceased activity for the remainder of the night. This pumping wing action was noted whenever an imago came to rest in a final sedentary position. It consists of movements of both wings approximately three times from the normal resting angle (Fig. 1, E) to a horizontal position (Fig. 1, F) and back again. It seems to be a tactile reflex movement associated with the imagos' preference for resting in crevices such as are furnished by corn leaf whorls.

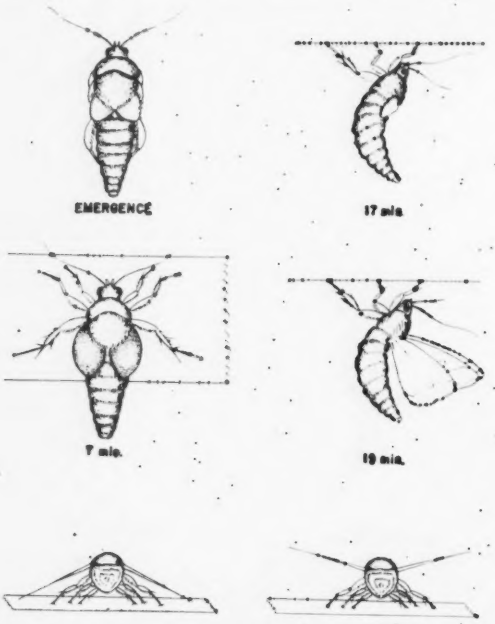


FIG. 1.—Behavior of the imago and expansion of wings after emergence from the pupa at approximately 80° F.

A. Position immediately after emergence. The wing-pads at emergence averaged about 6 mm. in length. Dorsal view.
B. Position after finding a suitable surface from which to hang. The insect remained in this position with unexpanded wing pads for approximately 17 minutes. Lateral view.
C. Position while the wings were undergoing expansion. The process of expansion took approximately 7 minutes. Dorsal view of insect from below.
D. Position while the wings were in the process of drying. At the end of the expansion period, the wings were snapped suddenly over the back and held tightly together for approximately 19 minutes. Lateral view.
E. and F. Movement of the imago's wings from the normal resting position (E) to a horizontal position (F) and back again. This reflex movement occurs three times as the moth arrives at a final sedentary position.

TABLE 1

HOURS OF EMERGENCE FOR 55 IMAGOS AT APPROXIMATELY 80° F., July, 1955

TIME	NUMBER OF IMAGOS	PERCENT OF TOTALS
5–6 p.m.	2	3.6
6–7 p.m.	0	0
7–8 p.m.	8	14.5*
8–9 p.m.	9	16.3*
9–10 p.m.	21	38.2*
10–11 p.m.	14	25.6*
11–12 p.m.	1	1.8
12–5 a.m.	0	0

*94.6 percent of total.

Observations were taken to determine the periods during the night when the imagos emerged. Table 1 shows that of 55 imagos observed, 94.6 percent emerged in the early hours of the evening from 7 p.m. until 11 p.m, with the largest number, 38.2 percent, emerging between 9 p.m. and 10 p.m. None emerged after midnight.

PERIODS OF NIGHT ACTIVITY OF THE IMAGOS

The question of when *H. zea* is most active is very important to an understanding of the

insect's nocturnal behavior. Quaintance and Brues (1905) stated that the period of activity began around 4 p.m. when the heat of day had passed. Their very extensive field studies showed, however, that often activity did not begin until 6 or 7 p.m., and that only when food was scarce were the moths out earlier. They also stated that the moths were quieter and shyer on clear evenings following hot dry days, and less active in cloudy or rainy weather, and that their flight was very swift early in the evening but gradually slowed down as night progressed. They also believed that imagos feed at night. This brings up the question of whether this moth is primarily crepuscular or nocturnal. The writer's observations in the field would seem to indicate that it is primarily crepuscular in its feeding habits and nocturnal in its oviposition habits. It is extremely difficult, however, to observe activity at night even by moonlight.

In order to determine what the periods of activity would be under controlled conditions where light and food supply were constant, the following experiments were conducted. The observation cage was equipped with a constant light source below 0.89 foot-candles, so that all activity took place at one intensity and not at varying intensities as would occur in the field. The activity of the moths in the cage was determined as follows: Each time 10 movements were noted, a mark was made. This would indicate 1 imago moving 10 times or 10 imagos moving once. The marks were totaled for each hour from 8 p.m. until 4 a.m. on two different nights and the average rounded off to the nearest tenth. Since the highest number of movements per hour was 70 and the lowest 0, the activity index from 1 to 7 was plotted on the figure ordinate (Fig. 2). Sometimes an imago would start moving and not stop for an hour or so; however, such movements were still counted as only one movement. An imago had to come to complete inactivity before it was counted again. Only 10 imagos were used, as more than that number could not be followed. The results showed that activity continued during the whole period of observation from 8 p.m. until 4 a.m. Actually the hood on the cage was open all day so the inactive period (broken line) represents daylight in the insectary. Imago activity had started by 8 p.m. when the low intensity light was turned on and hood dropped. There was a decrease in activity from around 9 p.m. until 11 p.m., then an increased activity for the remainder of the night until the drop after 3 a.m. The peak of activity at below 0.89 foot-candles was from midnight until after

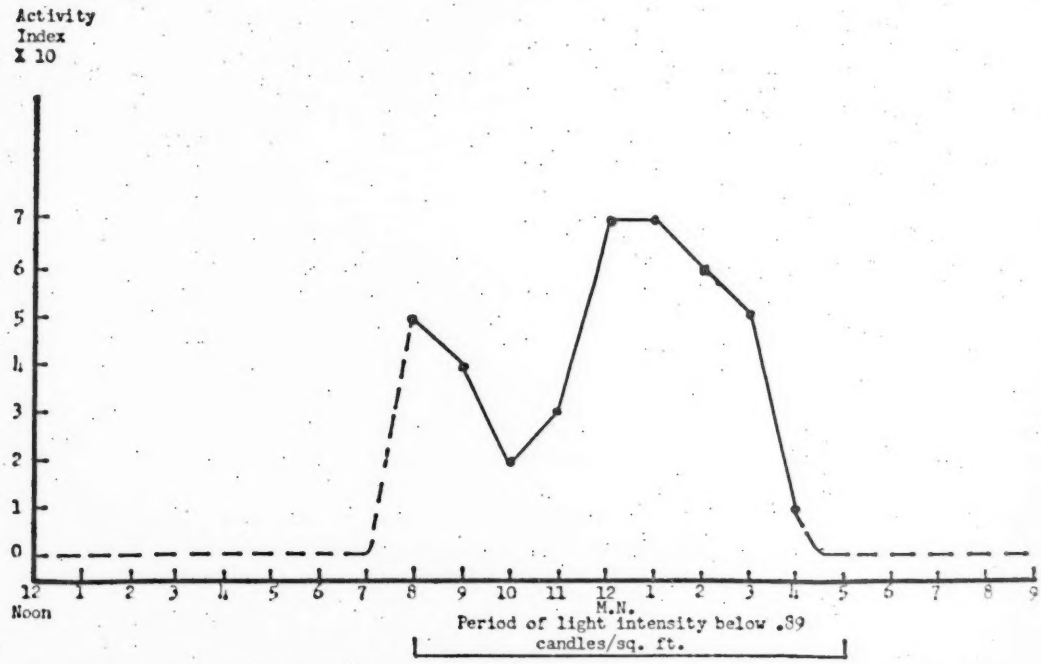


FIG. 2.—Average activity of the imago during 24 hour periods. The zero activity periods from approximately 12:00 p.m. to 8:00 p.m. and from 5:00 a.m. to 12:00 p.m. represented the daylight hours when the black hood was open on the behavior cage and the light intensity above 0.89 candles per square foot. (See text).

2 a.m. These data indicate that at this intensity, which might be termed a crepuscular intensity, the imagos remained fairly active for long periods. It did not show what the activity would be if the intensity were varied from daylight, through crepuscular intensities to darkness.

A second experiment was carried out with five imagos to determine what their reaction would be on going from a period of bright light to crepuscular intensity. These imagos were 5 from a group of 30 that had gone into diapause in November. The 30 had all been exposed as larvae and pupa to 16 hours of light per day but in spite of this, most of them did not emerge until spring. Use was made of the five that emerged during the second week of January, 1955. They were placed in a battery jar with paper over the top and a 40-watt bulb hanging over the paper, about 10 inches away. The battery jar was placed in a window where extraneous city light shone on the jar. The 40-watt bulb was left on all day and then turned off at successively later half-hour intervals between 7:30 p.m. and 10 p.m., on six different evenings, January 15 to January 20. The activities of the imagos were determined by the amount of noise made as the flying imagos hit the paper on top, after the 40-watt bulb was turned off. The only light then present was the extraneous light from the lights in town coming through the window. The results showed that on going suddenly from bright light to low intensities, there was an inactivity time lag of from 10 to 17 minutes (black bar, Fig. 3), followed by a period of considerable activity of from 17 to 45 minutes (white bar, Fig. 3). The activity continued for the remainder of the night, however, at a much lower pace (stippled bar, Fig. 3). These data indicate that the time of activity of the imago is not determined by some internal rhythm but depends upon stimulation after a certain period of time by low intensities of light.

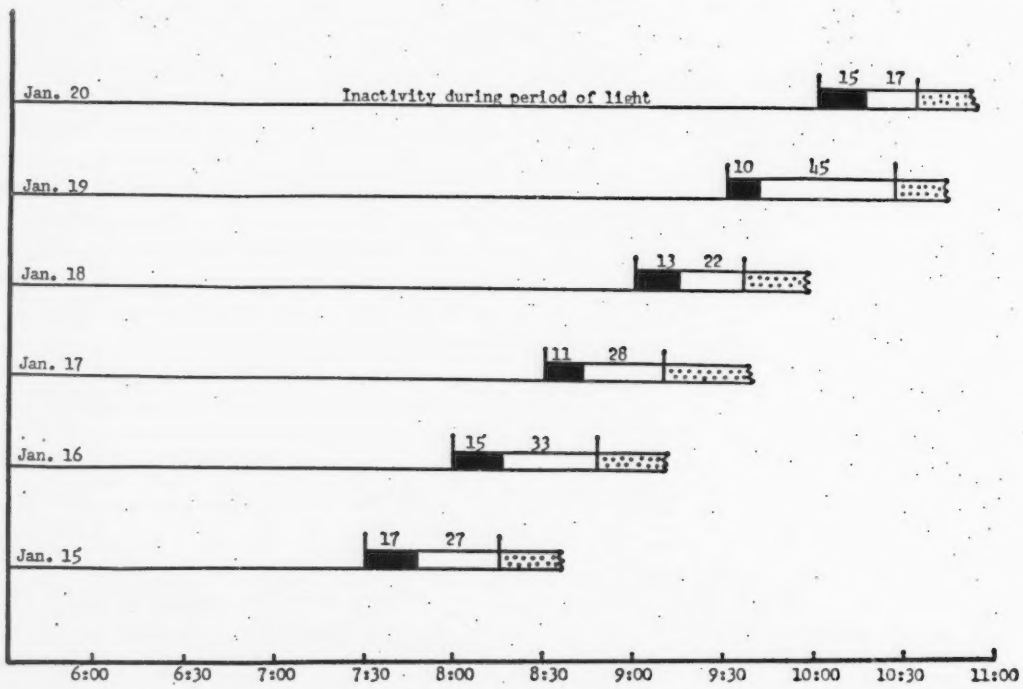


FIG. 3.—Time of reaction of five imagos subjected to continuous light which was turned off at successively later half-hour intervals between 7:30 p.m. and 10:00 p.m. from January 15 to January 20, 1955. The black bar represents inactive period after the light was turned off. The white bar represents the period of high activity and the stippled bar normal lower activity for the remainder of the night.

REPRODUCTIVE BEHAVIOR OF IMAGOS

The description of reproductive behavior is based on observations of reared imagos in the behavior cage. All activities took place at below 0.89 foot-candles. The imagos were placed in the cage the morning after their emergence date so all activity occurred from the first full day following emergence until death.

For about the first 10 minutes following the

darkening of this cage by the lowering of an observation hood, there was very little activity. After an average 10-minute time lag, several imagos would become active and begin flying to the color-lighted oviposition surfaces and the honey feeders. These few active imagos soon disturbed the other imagos and within half an hour most of them would be flying around. Before morning all the imagos would have visited the feeders at least once and would have fed for from 1 to 3 minutes. Copulation was never observed on this first complete night after emergence nor on emergence night.

On the second complete night after emergence, activity started in much the same way; however, on this and succeeding nights copulation was observed to take place along with feeding and exploration. Male imagos took the initiative in courting and by 1 a.m. most of the males would be very active, flying swiftly around the cage and especially back and forth between the color-lighted oviposition surfaces. At the most active period some of them could be observed landing on the surface and immediately extending their claspers 5 to 6 mm. out and curving their stretched abdomens sideways in a long arc. Females in the normal resting position were seldom disturbed. Some females, however, would be in an alert position with the wings held up and out at 45° angle and vibrating so swiftly that the edges appear only as a blur. In this position the abdomen of the female was exposed. A male landing beside such a female would walk as close to her side as possible and with his wings vibrating in a like manner would make a swift grab for the female abdomen with his extended genitalia. The female would pull violently away as the male attempted to hold from this side position. A struggle usually ensued with the male making as many as three grasps before he either fixed his hold or lost the female, which then flew away. If the male maintained his hold, the struggle subsided and they ceased activity for about a minute, then slowly moved around from a side position to an end position. For about the first 20 minutes of copulation they appeared to push against each other at approximately 15-second intervals, causing an up and down movement of their abdomens. The occurrence of the exposed abdomen of the female was important to successful copulation as it had been observed that females with crumpled wings that left the abdomen exposed were almost always successfully mated even though they were in a normal resting position and not in the alert position.

All copulations were observed to occur after 1 a.m. and to last between 1 hour to 1 hour and 45 minutes. Dissection for the spermatophore and observations on color-coded moths showed that the caged females had not copulated more than once. Males, however, were observed mating up to three different times and in one group of color-coded imagos of 26 females and 21 males, in which 15 females were mated, only 6 of the males were involved in all the matings.

After copulation the imagos separated by turning around sideways to each other and pulling apart. For about 5 or 10 minutes after separation, the imagos were very restless and flew around. After finding a secluded corner they usually pumped their wings up and down two or three times in their characteristic wing movement and settled down in a sedentary position for the remainder of the night.

TABLE II

PERCENTAGE OF MATINGS IN THE BEHAVIOR CAGE AS DETERMINED BY DISSECTIONS FOR THE SPERMATOPHORE

	Moths per Group	Females	Males	Females Copulated	Non-copulated	Percent
	47	26	21	15	11	58
	28	10	18	7	3	70
	28	16	12	7	9	43.4
Total	103	52	51	29	23	56

Percentage of Copulation of Caged Imagos and Time and Place of Copulation

All copulations were observed to take place between the second complete night after the emergence night and the seventh night. No copulation was ever observed on the night of the first emergence nor on the first complete night after emergence. Of 30 observed copulations, 29 took place on a color-lighted cloth oviposition surface and one occurred on the floor. This would seem to indicate that a physical attraction to the imago such as the colored surface increases the chances for copulation in a population, possibly because of increased proximity of the imagos attracted to the lighted surface. Records were kept on three different sized groups of imagos in the behavior cage with reference to the number of females that copulated. In one group, more males than females were put in the cage (Table II).

Previous records from the oviposition cages had

shown that 20 percent or less was the usual frequency of mating. The 56 percent success in this behavior cage may, therefore, have been attributable to the fact that so many imagos congregated at the 6-inch lighted oviposition surfaces. Just where these imagos mate in the field is unknown. No record of their copulating in the field has been found in the literature nor have night observations in the field produced any record. The data above indicate that a higher percentage of mating might be obtained by putting more males than females in the cage.

In the first group a pair of imagos were placed in each battery jar until 18 pairs were obtained that were ovipositing. Another group of 15 male and 7 female imagos were held with the sexes separate and averaged two in each battery jar. A third group of 19 males and 17 females were placed in holders (Fig. 4). Vials with a 10 percent honey solution were placed as food in the battery jars and the imagos in holders were fed the same solution twice a day from a small paint brush.

Table III gives the results of this experiment.

TABLE III

COMPARISON OF LENGTH OF LIFE OF PAIRED IMAGOS, UNPAIRED IMAGOS, AND IMAGOS HELD IN HOLDERS

Imago No.	Length of Life of Paired Imagos		Eggs Deposited No.	Length of Life of Unpaired Imago		Length of Life of Imago in Holder	
	Female	Male		Female	Male	Female	Male
	days			days		days	
1	4	6	3	5	1	8	5
2	5	6	30	5	2	9	10
3	7	6	178	6	3	10	11
4	7	7	500	6	3	12	11
5	7	7	138	6	4	13	12
6	7	7	210	6	5	13	13
7	7	7	300	7	5	15	13
8	8	8	13	—	5	15	14
9	9	8	83	—	5	15	21
10	9	9	407	—	5	16	25
11	9	9	150	—	5	17	—
12	10	9	18	—	6	22	—
13	10	9	247	—	6	24	—
14	10	10	4	—	9	24	—
15	10	10	112	—	13	24	—
16	10	11	189	—	—	24	—
17	13	11	70	—	—	25	—
18	15	12	12	—	—	—	—
Average Length of Life	8 3	8 4	2664	5 8	5 1	16 8	13 5

Average number of eggs deposited per female—148.

Longevity of Mated and Unmated Imagos and of Unmated Imagos Held in Holders

Norris (1934) showed in studies on *Ephestia kuhniella* that virgin females had an average life of 11.2 days while mated females had an average life of only 6.8 days. Since the length of life of the imagos was important in a knowledge of their oviposition potentiality, experiments were conducted to see if mated *H. zea* also had a shorter life than those that remained virgins.

It is well known that temperature has a great effect on the length of life of insects. However, since all these experiments were conducted at the same time in the insectary, the variation in temperature was the same for all the imagos. The imagos were broken up into three groups. These data indicate that there is no relationship between length of life and the number of eggs deposited. The results obtained for length of life for paired and unpaired earworm moths are the opposite of those obtained by Norris (1934) for *Ephestia kuhniella*. Several factors may be involved in these differences. Examination of six of the female moths showed that dead, unmated females had exhausted their fat bodies, while mated ones had a small portion of the fat body remaining. It has been noted while watching imagos at night that mated females always fed before or during oviposition while in the cage and spent more of their time at the feeder than unmated females. *Ephestia kuhniella* does not ordinarily feed. This may indicate that ovi-

positing *Heliothis zea* utilize less of the fat body and depend more on food gathered during adult life; however, this does not explain why the mated males also showed a longer life.

More important probably than the fact that they were mated or unmated was the amount of activity involved. The imagos in holders lived unnaturally long. It is doubtful if an imago in the field would ever live over 20 days, but this long life was not at all uncommon for held imagos. There seems to be an indication here that once an imago has mated, whether male or female, it becomes less active than those imagos that have remained unmated. In other words, the rate of activity of mated imagos slows down

FIG. 4.—Method for keeping moths stationary by suspending them with wings held in hair curlers.

while the activity of unmated imagos continues at a fast pace. This would not seem to hold for *Ephestia kuhniella*, but as mentioned before it does not feed as an imago so perhaps the virgin imagos lived longer by absorbing eggs that had not been deposited. This matter of absorption of eggs in unmated *Heliothis zea* is discussed more fully in another paper (Callahan, 1958). As the held imagos in this experiment were fed only twice a day and the caged imagos had access to food all night, it is very doubtful that they received less food than the held imagos. Observations at night have shown that most imagos visit a feeding station three or four times a night when active.

Oviposition Behavior of the Female Imago

Oviposition in every case started in each group of moths on the second complete night after the emergence night and usually at least one oviposition period occurred each night to the tenth or eleventh night at an average nightly temperature of approximately 82° F. The females rarely began oviposition without first feeding. About 8 p.m. oviposition began and usually continued for 40 to 50 minutes. This period was often broken by three or four short feeding trips. About 12 a.m. there was usually another 40- to 50-minute oviposition period and at about 2:30 a.m. a third and last period of ovipositing. Oviposition was an active process and the female, while looking for a spot to deposit eggs, arched the abdomen into a sickle shape and crawled rapidly over the surface. If the surface was suitably hairy, she stopped at 4 to 10 second intervals and extended the ovipositor straight down, pressing it against the surface. It took approximately 2 seconds to deposit one egg.

The laying of infertile eggs is often discussed in the literature. Quaintance and Brues (1905) stated that infertile eggs are laid very rarely in nature. As far as has been observed, *H. zea* never lays infertile eggs, caged or otherwise, in the sense that the laying of eggs or oviposition is a natural process. Unfertilized moths apparently absorb most of their eggs before they mature (Callahan, 1958). It is true that in cages infertile eggs have been obtained by most investigators. In all cases, however, there were many imagos in the cages, and dying female imagos can by reflex action alone squeeze a few, rarely more than 20, from their oviducts. Unmated females in clip holders have often held their tarsi to the tip of their abdomen while it is bent far forward under them. In this position mature ridged infertile eggs were often pressed out of the oviducts and deposited on the tarsi. A few infertile eggs have been obtained from each of five or six females held unmated in a single cage; however, none of the eggs were actually oviposited as done in nature.

Eggs were deposited in a characteristic arrangement around the outer edge of the circular cloth oviposition surface. Most of them were placed on the top edge, very few in the center of the circle of illuminated cloth, and very few on the glass or black sides of the cage. During oviposition the moths tended to circle the cloth along its circumference. As time went on, especially in the last few days of the moths' lives, more and more eggs were deposited on the floor of the cage. Two factors were probably responsible for this. One was the fact that the moths rested

TABLE IV

EGG COUNTS AT 1-HOUR INTERVALS FOR CAGE KEPT SUPPLIED WITH 10 FERTILIZED FEMALE EARWORM MOTHS BETWEEN JULY 7, 1956 AND JULY 27, 1956, BATON ROUGE, LOUISIANA

TIME	NEW MOON						FIRST QUARTER								FULL MOON							TOTAL
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
4:30– 5:30 p.m.	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	6
5:30– 6:30	0	1	0	0	0	0	3	10	15	0	0	0	0	7	1	1	0	0	0	0	0	41
6:30– 7:30	0	0	2	0	15	0	6	111	15	20	0	0	0	26	5	1	0	2	17	17	14	251
7:30– 8:30	0	0	4	14	32	143	198	101	48	30	1	0	10	159	0	2	35	177	41	163	11	1169
8:30– 9:30	5	9	23	15	16	101	227	31	22	29	5	2	78	98	7	31	24	16	23	32	0	704
9:30–10:30	0	33	13	10	12	89	246	1	25	24	9	8	153	144	12	38	20	5	87	44	0	975
10:30–11:30	0	32	26	12	14	88	115	8	13	12	0	21	139	99	16	11	51	2	50	52	0	764
11:30–12:30 a.m.	6	8	18	38	29	59	160	34	17	3	5	23	105	105	5	32	29	3	110	49	0	838
12:30– 1:30	12	14	30	13	20	35	140	16	21	6	1	70	151	62	0	41	33	2	93	16	0	774
1:30– 2:30	3	17	25	10	15	13	41	16	7	5	24	50	130	77	1	39	30	0	4	0	3	508
2:30– 3:30	21	31	8	4	24	5	26	23	2	3	9	86	102	86	8	54	1	1	10	8	10	522
3:30– 4:30	46	29	3	11	112	25	35	3	6	4	25	248	111	57	6	15	4	0	22	12	10	778
4:30– 5:30	12	4	28	13	70	5	16	3	10	0	29	177	61	22	9	12	0	0	15	3	5	494
5:30– 6:30	0	1	18	0	0	0	2	0	0	0	5	1	4	3	0	0	1	0	0	0	3	38
6:30– 7:30	0	0	0	0	0	0	0	0	0	0	5	0	1	10	0	0	0	0	0	0	0	16
7:30– 8:30	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	7
Total	105	184	196	140	359	559	1211	357	201	139	120	986	1018	958	73	280	228	208	472	396	56	7926

TABLE V

AGE, SEX RATIO, PERCENTAGE OF COPULATION AND OF MULTIPLE MATINGS FROM 6:00 P.M. TO 8:00 A.M. OF IMAGOS TAKEN AT A BLACK-LIGHT TRAP.

DATE	IMAGOS COLLECTED FROM THE TRAP			TOTAL FEMALES MATED	NO. OF SPERMATOPHORES TAKEN FROM FEMALES					PERCENT FEMALES MATED	AGE OF MATED FEMALES			AGE OF NON-MATED FEMALES			AVERAGE NIGHT TEMP. 6:00 P.M. TO 8:00 A.M.
	Total	Male	Female		1	2	3	4	5		1	2	3	1	2	3	
Sept. 29	53	20	33	9	7	2	0	0	0	27.2	—	—	—	—	—	—	71
Sept. 30	39	14	25	7	6	1	0	0	0	28.0	—	—	—	—	—	—	55
Oct. 3–4	29	12	17	6	3	3	0	0	0	35.3	0	5	1	3	8	0	63
Oct. 5–6	45	18	27	12	7	2	2	1	0	44.4	4	6	2	7	7	1	65
Oct. 7–9	141	54	87	27	18	8	0	1	0	31.0	1	22	4	1	47	12	52
Oct. 10	95	47	48	11	7	3	1	0	0	22.9	0	9	2	4	31	2	59
Oct. 12	187	78	109	71	34	24	8	2	3	65.1	0	53	18	0	28	10	65
Oct. 15–17	103	56	47	13	7	3	2	1	0	27.6	0	10	3	1	28	5	46
Oct. 18–19	145	64	81	16	9	2	5	0	0	19.7	0	13	3	0	59	6	45
Oct. 20–22	36	17	19	2	1	1	0	0	0	10.5	0	2	0	0	17	0	57
Oct. 24–28	50	22	28	10	6	4	0	0	0	35.7	0	8	2	0	16	2	36
Oct. 29–Nov. 1	7	2	5	1	1	0	0	0	0	20.0	0	1	0	0	4	0	45
Nov. 6–7	5	1	4	0	0	0	0	0	0	0.0	0	0	0	0	4	0	42
Total	935	405	530	185	106	53	18	5	3		5	129	35	16	249	38	

Sex ratios . . . 7.6 to 10.
Average percent females mated . . . 35%
Percent of single and multiple copulations . . . 57.3, 28.7, 9.7, 2.7, 1.6
Total and average percent of all copulations by females . . . 106 106 54 20 15 57%

Total 301

on the floor for longer periods and flew less as they got older, and the other was that as time went on, the floor collected more and more scales and trash until the floor itself presented an extremely hairy surface somewhat like the villous cloth preferred by the imago for oviposition (Callahan, 1957a).

Time of Oviposition of the Corn Earworm Moth

An automatic machine (Fig. 5) for collecting earworm eggs at 1-hour intervals consisted of a variable speed monodrum kymograph with a continuous paper assembly attached. The apparatus was arranged so the kymograph revolving at a speed of .607 foot per hour pulled a 6-inch-wide 12-foot-long bolt of white cloth across a 6" by 6" opening in a closed cage. The opening of the cage with the movable cloth was faced towards the east. The preference of the earworm moth for depositing eggs on a villous surface (Callahan, 1957a) enabled the eggs to be counted as all were deposited on the long bolt of villous white cloth passing slowly across the opening of the cage. The number of eggs laid per 1-hour interval during the night was calculated by counting the eggs the next morning on each .607 foot of cloth. This was the amount of cloth that passed the opening each one-hour period of the night.

The results (Table IV) indicate that the ovipositing females are active mainly during nocturnal periods rather than crepuscular periods and that egg deposition is continuous throughout the night with slightly more oviposition activity from 7:30 p.m. to 1:30 a.m.

Comparison of Sex Ratio and Percentage of Copulation of Reared Imagos With the Age, Sex Ratio, Percentage of Copulation, and of Multiple Matings of Imagos Taken From A Black-Light Trap

In order to determine if the reproductive potentiality in the cages was in any way indicative of what occurred in the field, all of the imagos collected in a black-light trap between September 29 and November 7, 1955 were placed in Bouin's picro-formol fixing fluid for 1 day and then transferred to 70 percent alcohol. Later these imagos were dissected, the sex determined, and the bursa copulatrix of each female dissected for a count of spermatophores. The females were

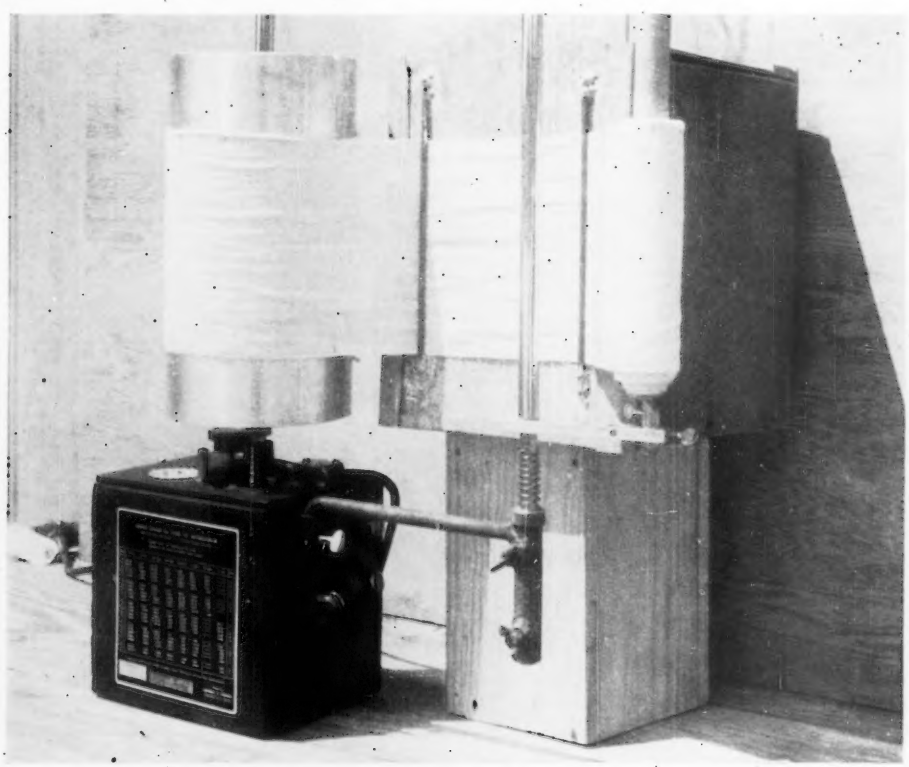


Fig. 5.—Kymograph machine used for determining time of oviposition of the corn earworm at night.

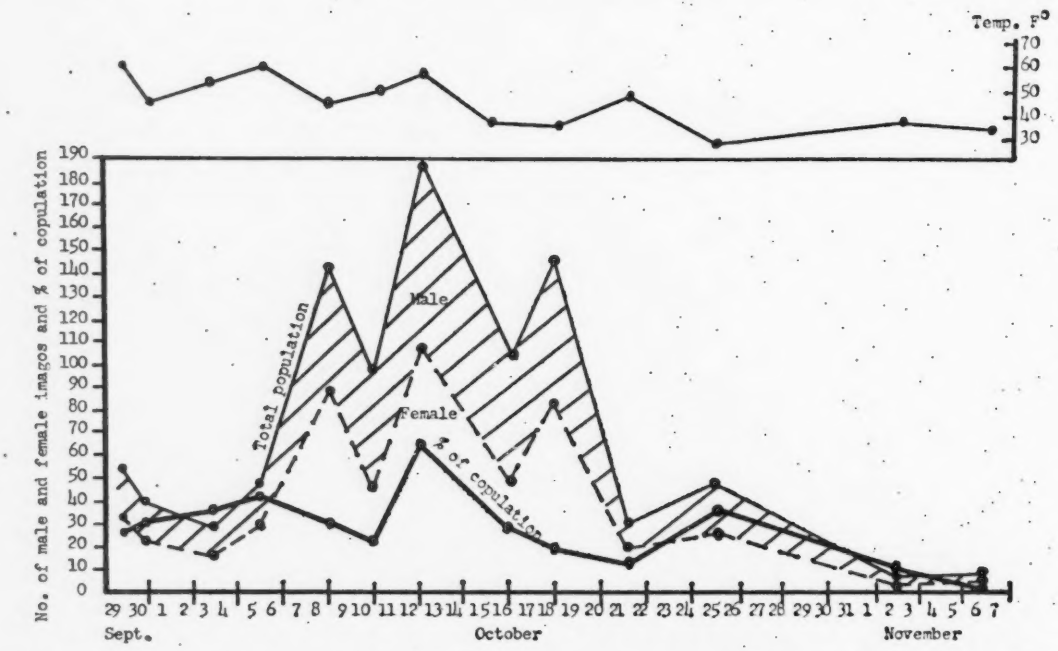


FIG. 6.—Sex ratio and percentage of copulation of imagos caught in the black-light trap from September 29 to November 6, 1955. The average nightly temperature between 6:00 p.m. and 8:00 a.m. for the period is also given.

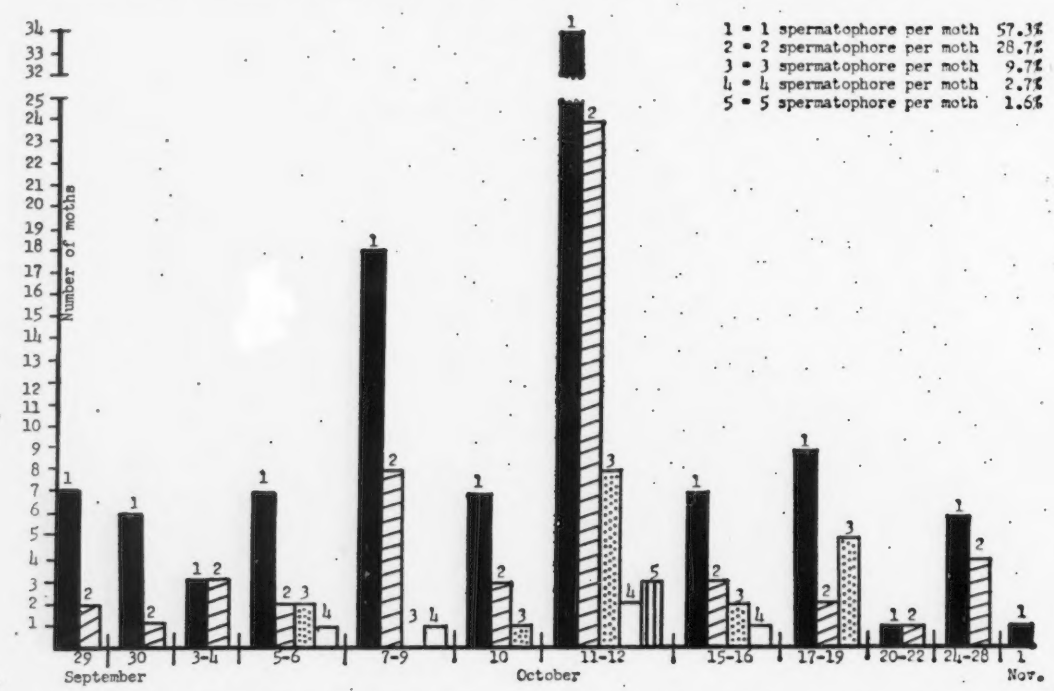


FIG. 7.—Histogram showing the number of single and multiple copulations for the mated imagos caught in the black-light trap from September 29 to November 1, 1955.

TABLE VI

FLOWERING PLANTS ON WHICH THE IMAGO OF *Heliothis zea* FEEDS. THE EXTENT OF BLOOMING PERIOD, ENVIRONMENT, AND COLOR OF FLOWERS WERE OBTAINED FROM GRAY'S MANUAL OF BOTANY OR THE AUTHORITY

PLANT AND AUTHORITY	COMMON NAME	BLOOMING PERIOD	ENVIRONMENT OF FLOWER	COLOR OF FLOWER
Robertson (1925):				
Solidago canadensis	Goldenrod	Aug. 1–Oct. 17	Moist, dry thickets	Yellow
Solidago graminifolia	Goldenrod	July 29–Sept. 29	Moist, dry thickets	Yellow
Solidago nemoralis	Goldenrod	Sept. 9–Oct. 18	Dry, open	Yellow
Bidens laevis	Bur-marigold	Aug. 6–Oct. 2	Marshes	Yellow
Bidens aristosa	Bur-marigold	Aug. 26–Oct. 17	Damp, low ground	Yellow
Aster multiflorus	Aster	Sept. 9–Oct. 22	Dry, open	White
Aster ericoides	Aster	Aug. 30–Nov. 8	Dry, open	White
Boltonia asteroides	Boltonia	Aug. 8–Oct. 4	Sandy thickets	White
Polygonum pensylvanicum	Pinkweed	June 20–Oct. 26	Damp thickets	Pink
Nuttycombe (1930):				
Trifolium arvense	Rabbit-foot clover	June 6–July 17	Cultivated fields	White
Trifolium pratense	Red clover	June 6–Oct. 3	Meadows	Roseate
Trifolium repens	White clover	June 6–Sept. 28	Meadows	White
Trifolium agrarium	Hop clover	June 6–July 10	Dry fields	Yellow
Cephalanthus occidentalis	Button-bush	July–Aug.	Marshes	White
Nepeta cataria	Catnip	June–Sept.	Roadsides	White
Rudbeckia sp.	Cone-flower	July 20–Sept. 23		Yellow
Vigna sinensis	Cowpea		Cultivated fields	Purple
Chrysanthemum sp.	Daisy	June 6–Oct. 3	Fields and roadsides	Yellow
Anthemis cotula	Dog-fennel	June 25–Aug. 14	Fields and roadsides	White
Erigeron sp.	Erigeron	June 6–Oct. 3	Fields and roadsides	White
Medicago sativa	Alfalfa	June 6–Oct. 3	Cultivated fields	Purple
Solanum carolinense	Horse-nettle	June 25–Oct. 3	Sandy openings	Violet
Apocynum cannabinum	Indian hemp	June 20–Sept. 13	Open ground	White
Eupatorium purpureum	Joe-pye weed	Aug. 6–Sept. 26	Woods	Pink
Achillea millefolium	Milfoil	June 6–Sept. 13	Fields and roadsides	Roseate
Asclepias syriaca	Milkweed	June 17–Aug. 19	Dry fields	Purple
Aster sp.	Wild aster	Sept. 4–Oct. 3		
Daucus carota	Wild carrot	June 10–Sept. 27	Dry fields	White
Allium vineale	Wild onion	June 20–July 30	Grasslands	Purple
Vicia sp.	Wild vetch	June 6–Aug. 9		
Quaintance and Brues (1905):				
Hibiscus gossypium	Cotton	July–Sept.	Cultivated fields	White
Eupatorium scrotinum	Joe-pye weed	Aug.–Oct.	Moist, dry thickets	White
Helianthus sp.	Sunflower	July–Nov.	Fields and roadsides	Yellow
Solanum rostratum	Kansas-thistle	July–Oct.	Plains	Yellow
Prunocerasus sp.	Plum blossom	April–June	Orchard	White
Garman and Jewett (1914):				
Melilotus alba	Sweet clover	May–Oct.	Rich soil	White
Pepper (1943):				
Phaseolus limensis	Lima bean	July–Aug.	Cultivated fields	Purple
The author:				
Nicotiana tabacum	Tobacco	Aug.–Sept.	Cultivated fields	Greenish
Phaseolus vulgaris	Bush bean	July–Aug.	Cultivated fields	Purple
Petunia sp.	Petunia	June–Sept.	Garden	Purple
Amphicarpa bracteata	Hog-peanut	Aug.–Sept.	Damp, woodlands	Purple
Datura stramonium	Jimsonweed	July–Oct.	Dry, waste ground	Lavender
Ipomoea purpurea	Wild morning glory	June–Oct.	Corn fields	White
Tribulus terrestris	Puncture vine	June–Sept.	Dry, waste ground	Yellow

also classified as to approximate age by observations on the fat body where "one" equaled young imagos with all the fat body, "two" equalled middle period imagos with the fat body half depleted, and "three" equaled old imagos with all the fat body depleted (Callahan, 1958). Temperatures were also recorded to find out whether temperature had any effect on the percentage of copulation. The temperature was calculated using Strachey's formula (Shelford, 1929) for computing average day-degrees when only maxima and minima are given and when both minima are above zero:

$$X = \frac{a+b+2c}{4}$$

where X = average day-degrees
a = first minimum, degrees above 0°
b = second minimum, degrees above 0°
c = maximum, degrees above 0°

The maximum and minimum temperatures were taken at 2-hour intervals from 6 p.m. until 8 a.m. and two lowest and one highest for the 8-hour period substituted in the formula. The temperature, age, sex ratio, and percentage of copulation are all shown in figure 6 and Table V.

These data show the sex ratios for 935 trapped imagos to be 7.6 males per 10 females while the ratio for 154 reared imagos was 8.3 males per 10 females; also for any one date from the light trap, the female catch was higher than the male catch, except for October 15–17. In general, the sex ratios from day to day remained about the same (Fig. 6). The percentage of females that had mated was 35 percent for the light trap and 56 percent for the reared imagos. However, the percentage for the number of actual copulations as determined by the number of spermatophores in each female was 57 percent for the light trap and 56 percent for the reared imagos, as all reared imagos had only one spermatophore. This figure for the reared imagos was taken from 52 of the 84 females on which the sex ratio was based, as only 52 were dissected for spermatophores. However, in other experiments over 100 female imagos had been dissected and never more than one spermatophore was found at any time. Just why there were from one to five copulations for a single field collected imago and only one for every reared imago is unknown. The histogram (Fig. 7) shows the number of spermatophores taken from female imagos on the various dates. Of these, 57.3 percent had one spermatophore, 28.7 percent had two, 9.7 percent had three, 2.7 percent had four, and 1.6 percent had five spermatophores.

From September 29 until the middle of October the percentage of mated females increased as the night temperature increased, and decreased as the night temperature decreased. This may have been a function of the larger population flying during the warmer periods (Fig. 6). As the temperature dropped into the forties, however, the above did not hold.

Table V shows that of the mated females, 129 were middle age while only 5 were very young and 35 older. Of the non-mated, 249 were middle age, 16 very young, and 39 older. It would seem from these data that most of the imagos attracted to the light trap were in the optimum reproductive stage. Probably the very old imagos would not be able to reach the trap anyway, as in cages they usually deposit their last few eggs on the floor of the cage. It is believed that, since most of these imagos were in the middle reproductive stage, the population at the light trap probably was a fairly representative sample of percentage of mating and copulation and of sex ratios of imagos for the cooler temperatures of October. The lower sex ratio of males in the field would be expected as there was a much greater loss of males to disease, etc., while rearing them.

FLOWERING PLANTS ON WHICH THE IMAGO FEEDS

There are many lists and references throughout the literature to the host plants on which *H. zea* larvae feed or on which the adults oviposit. Very few references, however, record specifically whether the imago was observed feeding on the flowers or nectaries of the plants. The fact that an imago is attracted to a plant for feeding does not necessarily mean that the same plant is suitable for oviposition. As Quaintance and Brues (1905) pointed out, the imago is drawn to cowpeas by the material secreted by the glands on the fruit stalks but oviposition is very uncommon on such plants. Table VI gives a list of plants upon which authors definitely state the imago feeds and upon which the imago was observed feeding. The extent of blooming period was taken either from the authority or from Gray's Manual of Botany. The environment and color of the flowers were taken from Gray's Manual alone.

It may be seen from the list that *H. zea* visits almost every possible environment during its feeding excursions. The blooming period of plants the imago visits extends throughout the season from May to November. The predominance of white and yellow flowers visited is probably due to the greater number of American species with white and yellow hues and not to the color itself. Lutz (1924) gave the percentages of 3000 insect- or self-pollinated flowers as 32 percent white and 27 percent yellow or 59 percent of all the colors. Green made up 8 percent, red 8 percent, purple 14 percent, and blue 11 percent of all the species. He further stated that most yellow flowers and many red and purple flowers are strongly ultraviolet in reflection while white and blue are not, and that both white and yellow flowers reflect large amounts of red. From these statements it would seem difficult to attach

more significance to one or two flower colors than to the rest.

REFERENCES CITED

Callahan, P. S. 1957a. Oviposition response of the corn earworm to differences in surface texture. Jour. Kansas Ent. Soc. 30: 59–63.

1957b. Oviposition response of the imago of the corn earworm, **Heliothis zea** (Boddie), to various wave lengths of light. Ann. Ent. Soc. America 40: 444–52.

1958. Serial morphology as a technique for determination of reproductive patterns in the corn earworm, *Heliothis zea* (Boddie). In press.

Fernald, M. L. 1950. Gray's manual of botany, 8th edition. 1632 pages. New York: American Book Company.

Garman, H., and **H. H. Jewett.** 1914. The life history and habits of the corn earworm. Kentucky Agric. Expt. Sta. Bull. 187: 511–91.

Lutz, F. E. 1924. Ultra-violet and flower visiting habits. Ann. New York Acad. Sci. 29: 181–283.

Norris, Maud J. 1934. Contributions towards the study of insect fertility III. Proc. Zool. Soc. London, 333–60.

Nuttycombe, J. W. 1930. Oviposition of the corn earworm moth in relation to nectar flow of some flowering plants. Jour. Econ. Ent. **23:** 725–8.

Pepper, B. B. 1943. The relationship between cropping practices and injury by *Heliothis armigera* with special reference to lima beans and tomatoes. Jour. Econ. Ent. **36:** 329–30.

Quaintance, A. L., and **C. T. Brues.** 1905. The cotton bollworm. U. S. Dept. Agric. Bull. 50, p. 155.

Robertson, Charles. 1928. Flowers and insects, lists of visitors of four hundred and fifty-three flowers. Carlinville, Ill. Lancaster, Pa. Science Press.

Shelford, Victor E. 1929. Laboratory and field ecology. Baltimore: Williams and Wilkins Co.

FEEDING AND NUTRITION OF THE MILKWEED BUG, ONCOPELTUS FASCIATUS (DALLAS)[1]

STANLEY D. BECK, C. A. EDWARDS,[2] AND JOHN T. MEDLER

Department of Entomology, University of Wisconsin, Madison

ABSTRACT

Feeding behavior of fifth-instar nymphs was studied utilizing a photographic technique with exposures on color film made, usually, at 60-second intervals. On the natural diet of milkweed seed, feeding occurred in cycles averaging about 22 hours, separated by inactive intervals of 2 to 6 hours. Feeding activities occupied about 75% of each major feeding cycle. No feeding was done during the 48 hours preceding the imaginal (final) ecdysis. Intensity of feeding and characteristics of feeding behavior were markedly influenced by the presence or absence of the milkweed seed coat. The seed coat factors important to normal feeding have not been identified, but are presumed to be chemotactic in nature. The apparent deficiencies of a purified diet developed in earlier work were shown not to be nutritional; instead, they were related to a failure of this diet to meet the feeding requirements of the bug.

INTRODUCTION

The culturing of a plant-feeding insect under artificial conditions and on purified or synthetic diets may pose problems involving many factors in addition to the nutritional requirements of the insect. The physical and chemical feeding requirements of the insect must be met, and the failure of the insect to survive or grow on a given synthetic diet is not necessarily an indication that the diet is nutritionally deficient. The plant-sucking forms have proved to be very difficult to rear apart from a host plant, although a number of workers have devised techniques for maintaining them for relatively short periods under artificial experimental conditions (Carter 1927, Hamilton 1935, Maltais 1952, and others). It has not been at all clear whether the short survival of the insects was the result of a failure to satisfy their nutritional or their feeding requirements. Two species of plant bugs, *Oncopeltus fasciatus* (Dallas) and *Euschistus variolarus* (P. de B.), were reared from egg to adult under laboratory conditions on purified diets by Scheel *et al.* (1957). The growth obtained was distinctly suboptimal, however, as the diet-reared bugs required about twice as long to attain maturity and their adult weight averaged only half as much as the control bugs reared on natural diets.

The present study was undertaken to determine whether the subnormal growth of *Oncopeltus fasciatus* nymphs on purified diets was to be accounted for on the basis of the insect's nutritional requirements or its chemical and physical feeding requirements. This research necessitated the development of a technique for obtaining quantitative data on the feeding behavior of the bugs. The method devised should be applicable to a variety of insect problems, with perhaps only slight modification of feeding chamber and optical system.

METHODS AND MATERIALS

A stock culture of milkweed bugs was main-

[1]Approved for publication by the director of the Wisconsin Agricultural Experiment Station. This research was supported in part by a grant from the National Science Foundation. The technical assistance of Messrs. E. T. Kaske and L. G. Wilson is gratefully acknowledged. Accepted for publication December 14, 1957.

[2]Present address: Entomology Department, NAAS, Government Buildings, Westbury-on-Trym., Bristol, England.

tained on milkweed seed and water in large battery jars. To obtain nymphs for experimental use, subcultures were started periodically from groups of eggs produced by the stock cultures. The subcultures were also maintained on milkweed seed and water. At the last nymphal molt, individual nymphs were isolated and, in most experiments, were held for 24 hours with access to water but not to food. These 24-hour postmolt, unfed, fifth-instar nymphs are referred to below as "standard bugs."

The feeding activity of the standard bugs was recorded photographically with a Kodak Cine Special II 16-mm. movie camera and a Samenco Movie Control timer (Figure 1A). The timer also controlled the lights, and was adjusted so that the lights came on for one second, during which the shutter was tripped to expose one frame. In most experiments, a 60-second interval between exposures was used. The timing error inherent in the equipment was slightly less than 2 percent at the 60 second setting. The camera lens was a 25-mm. F/1.9 Cine Ektar with a spacing ring added to decrease the field size. The film used was Kodackrome type A, artificial light. In preliminary experiments, black and white films of several types were tried, but it was found that color film gave better resolution and was more easily analyzed on the film reader. Fixed interval exposure made it possible to determine the duration of feeding by counting frames, but this proved very laborious. Including a wristwatch in the photographed field permitted easier and more accurate measurements of the time factors involved in the various aspects of feeding behavior.

The chambers in which the experimental insects were confined consisted of stender dishes half-filled with paraffin. A hole was cut through the wax layer at the center of the dish by means of a cork borer, and an absorbent cotton wick was fitted into the hole. In most experiments, the wick was moistened with water, but in some cases it was moistened with a liquid experimental diet. Shallow holes were cut in the surface of the wax to accomodate moistened granular purified diets. When milkweed seeds were fed, they were pressed into the wax just sufficiently to prevent their being moved about by the nymphs. The feeding arrangement is shown in Figure 1B.

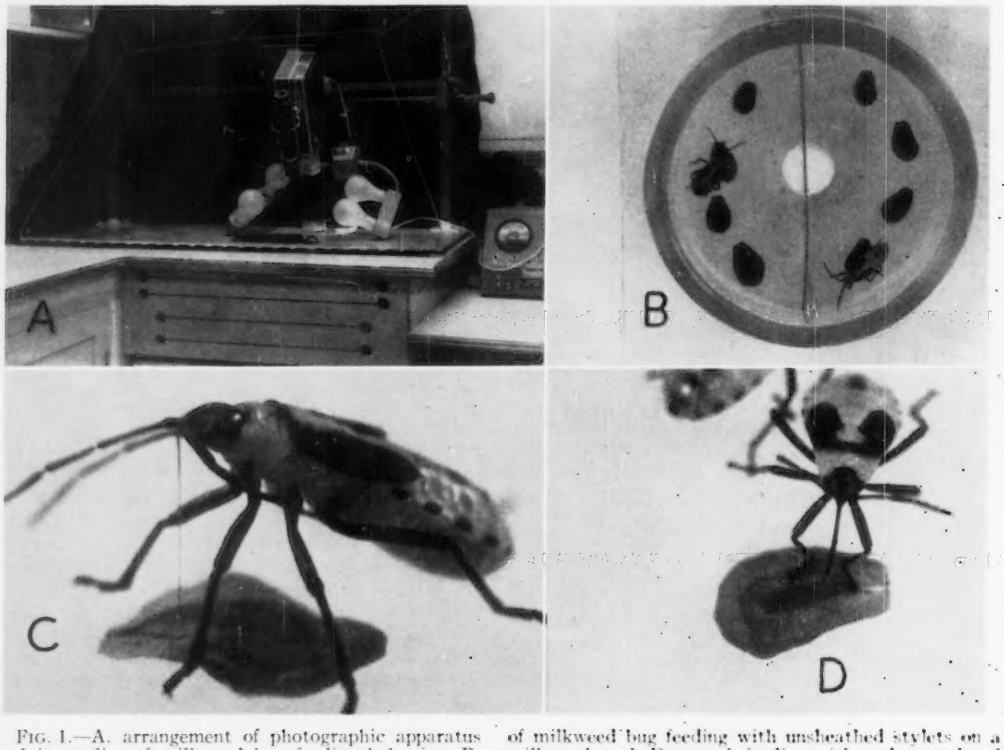


FIG. 1.—A. arrangement of photographic apparatus used in studies of milkweed bug feeding behavior; B. partitioned feeding chamber for experimental studies of nutritional requirements and feeding behavior; C. nymph of milkweed bug feeding with unsheathed stylets on a milkweed seed; D. nymph feeding with stylets enclosed in the labium.

The lid of the stender dish was replaced by a section of flat transparent plastic. A small hole was cut in the plastic cover immediately above the moist wick; if this precaution was not taken, water vapor accumulated above the wick and clouded the picture.

Two standard bugs were marked with white ink for identification and placed in the feeding chamber. More than two nymphs in the same chamber made film interpretation difficult, because they tended to congregate on one seed or diet, obscuring the camera view of all. A plastic partition was sometimes used to keep the bugs separated (as in figure 1B). A black cloth was thrown over the set up to cut out extraneous light during the experiments. The experiment was allowed to run 22 hours. This time was selected in preference to 24 hours because of exposure rate and film length. Sixteen millimeter film has 40 frames per foot, and exposing 1 frame per minute expends $1\frac{1}{2}$ feet per hour. Three 22-hour experiments can be recorded on one 100-ft. roll of film, whereas three 24-hour experiments would require more footage.

After the film was exposed and developed, it was examined on a Remington Rand Model 9 microfilm reader. The proboscis of a feeding nymph was clearly visible on the film. Frame-by-frame analysis of the film record yielded data on the number of feeding attempts, duration of feeding, duration of non-feeding periods, and the nature of the feeding cycle during the experimental period or any arbitrary fraction thereof. The film records also provided information on the behavior patterns associated with feeding, the effect of physical and chemical factors on feeding, the rate of food consumption, and the effect of intra-stadial development on feeding.

The purified diets used in the nutrition and feeding experiments are shown in Table I. The purified diet shown is that of Scheel *et al.* (1957), modified only by a slight increase in water content. In some experiments artificial milkweed seeds were used. These were made by placing small amounts of the purified diet in shallow holes in the paraffin floor of the feeding chamber and then sealing the holes with the husks of empty milkweed seeds. The nymphs penetrated the husks readily and fed on the diet beneath. In addition to these diets, an aqueous infusion of green milkweed pod was used in a few feeding experiments. The pod infusion and liquid purified diets were fed to the bugs from cotton wicks.

RESULTS

Before attempting to measure the effects of purified diets on the feeding behavior of *Oncopeltus fasciatus* (Dallas), a study was made of their behavior on milkweed seed. A number of aspects of their feeding were considered pertinent to the basic problem being investigated: (1) frequency of feeding; (2) duration of feeding; (3) influence of developmental stage on feeding; and (4) quantity of food consumed per unit time. Information on these points was obtained from experiments in which photographic records were taken of the activities of nymphs during the entirety of the fifth (last) nymphal stadium. The timer and camera unit was started during ecdysis and was run until imaginal ecdysis occurred. The nymphs had access to milkweed seeds and water at all times and were disturbed only at the time of a daily replenishing of their food and water supply. An average of 140 hours elapsed between the two ecdyses. The record of their feeding activity during the stadium is shown in Figure 2.

TABLE I

COMPOSITION OF PURIFIED DIETS USED IN NUTRITION AND FEEDING BEHAVIOR STUDIES OF *Oncopeltus fasciatus* (DALLAS)

CONSTITUENT	AMOUNT USED	
	Purified Diet (gm.)	Liquid Purified Diet (gm.)
Dextrose	5.00	2.00
Soluble starch	5.00	2.00
Sodium caseinate	5.00	2.00
Corn oil	1.00	0.80
Cholesterol acetate	0.20	0.10
Mineral salts[a]	0.50	0.10
Brewers yeast powder	4.00	—
Yeast hydrolysate	—	1.00
B-vitamin mixture[b]	—	2.00 (ml)
Water	21.0 (ml)	98.00 (ml)

[a] "Salts W", Nutritional Biochemicals Corporation

[b] See Beck (1953) for composition of vitamin solution.

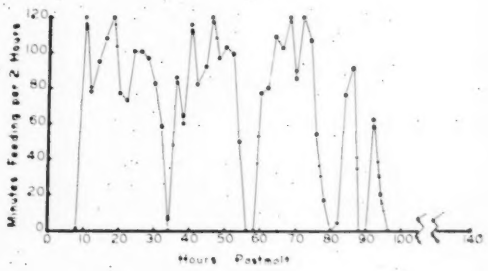


FIG. 2.—Feeding activity of fifth-instar milkweed bugs on seeds of milkweed.

The data presented in Figure 2 were compiled from the film record of a single bug rather than from the averages of the several replicate experiments. Although the feeding record shown is typical, the individual nymphs varied somewhat in the duration of the feeding cycles, making it difficult to plot a meaningful average. It should

also be pointed out that the bugs were assumed to be actively feeding whenever the proboscis was visibly inserted in a seed in two or more successive photographs. An isolated frame of a bug in a feeding position was not counted in feeding time, but was considered to be possibly part of a probing behavior pattern. In no case did feeding occur earlier than eight hours after ecdysis. After this, feeding was quite intense, although distinctly cyclic until about the 80th postmolt hour, after which it declined rapidly. No feeding occurred from about the 96th hour until the final ecdysis at about the 140th hour. The major feeding cycles were from 20 to 24 hours duration with periods of from 2 to 6 hours of relative inactivity between them. After about 80 hours the feeding cycles became very much shortened.

During a major feeding cycle, feeding was interrupted occasionally by the bug's abandoning the seed on which it was feeding and visiting the cotton wick for a short (5 to 15 minute) period of ingesting water. The bug would then usually return to the same seed on which it had been feeding. As a seed became depleted, feeding was interrupted with increasing frequency until it was finally abandoned. A new seed was then attacked. Examination of abandoned seeds showed that the entire endosperm had been consumed; only the embryo was left. There was no evidence of digestion of the seed coat. A seed was depleted by from 200 to 400 minutes of feeding, depending on the size of the seed kernel. During the periods of intense feeding, fifth instar nymphs consumed an average of two and a half seeds per 22-hour feeding cycle. This amounted to about 9 milligrams of seed tissue per day.

Experimental determination of the effects of different diets on nymphal feeding behavior involved the use of standard nymphs, insuring uniformity of developmental stage and immediate nutritional history. The "standard bugs" began feeding very soon after being introduced in the experimental feeding chamber, and fed intensely for the entire 22-hour experiment, at least in those cases where the diet offered was milkweed seeds. The effects of some different diets on the characteristics of nymphal feeding are summarized in Table II.

TABLE II

EFFECTS OF DIFFERENT DIETS ON THE FEEDING BEHAVIOR OF FIFTH INSTAR NYMPHS OF THE MILKWEED BUG, *Oncopeltus fasciatus* (DALLAS)

DIET	AVERAGE 20 HR. TOTAL FEEDING	AVERAGE 20 HR. TOTAL FEEDING ATTEMPTS	AVERAGE FEEDING DURATION
	(min.)	(No.)	(min.)
Milkweed seed	911	27.4	35.3
Liquid diet	110**	4.0**	26.0
Purified diet	314**	16.0**	22.1*
Artificial seeds	896	24.6	37.6
*LSD .05	115	7.2	13.1
**LSD .01	156	9.6	17.6

The purified diet, on which Scheel *et al.* (1957) showed that the milkweed bug could be reared, induced only about one third as much feeding as did milkweed seed. There were significantly fewer attempts to feed, and the average feeding duration was significantly less than on milkweed seeds. Andre (1934) found that the milkweed bug is not exclusively a seed feeder, but will feed on the succulent parts of milkweed as well. As shown in Table II, however, a liquid diet offered in a cotton wick was not at all conducive to feeding. Artificial seeds in which purified diet was covered with the husk of a milkweed seed resulted in feeding behavior which was indistinguishable from that evoked by milkweed seed. The influence of milkweed seed, purified diet, and artificial seed on the feeding pattern of standard bugs is shown in Figure 3. The intensity and persistence of feeding on artificial seeds (AS) was essentially identical to that on milkweed seed (MWS). On purified diet (PD) the feeding was in the form of a series of short cycles. During the active phases, feeding was not of normal intensity or duration. The nonfeeding phases lasted from two to several hours. The importance of the seed husk to milkweed bug feeding was forcibly demonstrated by these results.

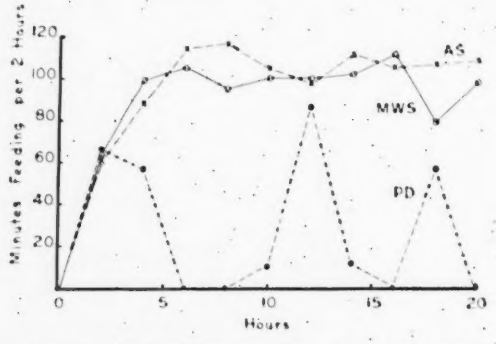


FIG. 3.—Effect of different diets on feeding of milkweed bug nymphs. MWS=milkweed seeds; AS=artificial seeds; PD=purified diet.

The exact role of the seed husk in milkweed bug feeding has not yet been elucidated. However, the results obtained thus far indicate that the importance of the husk is more than that of a simple supporting membrane. Covering the purified diets with either complete or perforated membranes did not improve feeding. The nymphs did not feed through an impermeable membrane. On a perforated membrane they probed through the perforations to feed on the diet below, but

feeding was no more frequent or intensive than on uncovered purified diets. Observation of the nymphs under different feeding conditions indicated that feeding was always preceded by exploratory probing with the proboscis before the stylets were used to penetrate the seed coat or diet surface. It seems likely that tactile organs and chemoreceptors on the tip of the labial sheath contribute to the selection of the feeding site. Once the dietary substrate has been penetrated by the stylets, the labial sense organs may not be of major importance in the maintenance of feeding. It was frequently observed that once the nymph was feeding, the labium became separated from the rest of the mouthparts and was returned to its normal resting position along the ventral side of the insect (Fig. 1C). Feeding was continued with only the hair-thin stylets penetrating the seed or diet. This "stylet feeding" behavior strengthens the hypothesis that feeding maintenance is influenced separately from orientation and probing. Study of filmed records of feeding showed that the nymphs invariably fed with the anterior tarsi on the seed or diet on which it was feeding, except when only the stylets were in use, as in Figure 1C. Figure 1D shows the typical feeding position of a fifth instar nymph. Although it has not been demonstrated as yet, it seems likely that tarsal sense receptors may play a role in feeding behavior.

In an earlier report of our work on the nutrition of plant-sucking Hemiptera (Scheel *et al.* 1957), it was suggested that the suboptimal growth obtained on the purified diet might be the result of a failure to meet the insects' feeding requirements. The experiments run in that study were of the usual nutritional type in which the criteria of dietary adequacy were growth and survival of the insects. Such experiments did not allow a distinction between nutritional and behavioral effects. The feeding behavior experiments discussed above demonstrated that the purified diet did, indeed, fail to meet the feeding requirements of the milkweed bug nymphs. Its inadequacy in this regard was completely corrected simply by covering the diet with milkweed seed husks. It became of considerable interest to test the artificial seed diet for nutritional adequacy. Accordingly a series of experiments was run in which first instar milkweed bugs were started on milkweed seeds, artificial seeds, or purified diet. They were weighed periodically and the growth curves obtained are shown in Figure 4. The growth of the nymphs receiving the purified diet was poor and none reached the fourth instar during the 22 days of the experiments. Growth on the artificial seeds was normal until the fifth nymphal instar, at which time about one-third of the nymphs died. This late mortality occurred after feeding had been completed and at about the time the final molt should have taken place. Those that attained adult status were of lower average weight (57.4 mg.) than the adults obtained from the milkweed seed diet (67.5 mg.). This difference was found to be highly significant statistically. The adults from the artificial seed diet mated and produced viable eggs. The truncated growth curve and late mortality were indicative of a slight nutritional deficiency in the artificial seed diet.

Examination of the artificial seeds after the nymphs had fed on them always showed the diet either partially or completely consumed. The husks displayed no signs of digestion, but showed small holes cut by the piercing mouthparts of the nymphs. It seems highly unlikely that the insects obtained a dietary growth factor from the seed husks. The striking effect of the husks on nymphal growth must be attributed to an increased dietary uptake stimulated by physical or chemotactic factors associated with the husk of the seed.

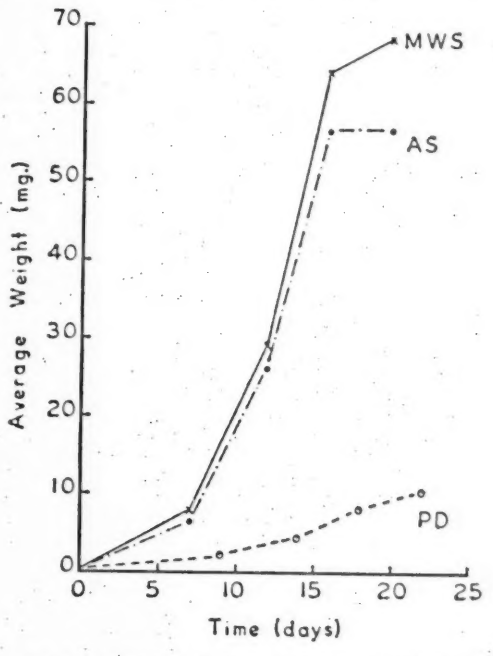


FIG. 4.—Growth of milkweed bugs on milkweed seed (MWS), artificial seeds (AS), and purified diets (PD).

Oncopeltus fasciatus (Dallas) is essentially a monophagous insect. It was found feeding only on milkweed species by Andre (1934). Blatchley (1926) reported also finding adults on willow and golden rod, but apparently it was not utilizing those plants as hosts. Hussey (1952) has reported that oleander serves as a host plant in Florida. Andre observed that the bugs would occasionally pierce the tissues of grass-plants,

but he could not rear them on such hosts. His interpretation was that plants other than milkweed were sometimes utilized as sources of water in instances where their feeding was primarily on dry or nearly dry milkweed pods. The milkweed bug feeds successfully on either the succulent parts or the mature seeds of milkweed. The facultative seed-feeding characteristic makes the insect a simpler experimental animal than are species which feed only on succulent plant parts, but has also confused the picture somewhat in regard to the bug's nutrition and host specificity. A number of workers have attempted to rear the milkweed bug on various seeds and nuts. Lea and Neiswander (1950) tried dried raisins, kidney beans, oats, pumpkin, squash, and watermelon. They found that the bugs would feed and grow on cracked watermelon seeds. Frings and Peissner (1952) reared milkweed bugs through several generations on blanched peanuts and reported that growth, survival, and reproduction were as good as on milkweed seed. This claim was later recanted (Frings *et al.* 1957), and it was pointed out that blanched peanuts were much inferior to milkweed seed for both survival and reproduction. Scheel (1956 unpublished thesis) reared milkweed bugs on a number of different kinds of nuts and found all of them to be inferior to milkweed seed for nymphal growth and survival. The nuts tested were, in order of decreasing value as milkweed bug diet: black walnuts, almonds, English walnuts, peanuts, pecans, and Brazil nuts. The interest in searching for a seed or nut which is satisfactory substitute for milkweed seed arose from the inconvenience of procurring an adequate supply of milkweed seed. The degree to which different seeds and nuts may prove to be satisfactory as dietary substrates yields no information on either the nutritional requirements or the feeding specificity of the insects. The total effectiveness of a given diet must be considered as a result of both the nutritional and behavioral aspects of the insect's adaptations to a natural diet. Of the two types of requirements, behavioral satisfaction must precede any sort of nutritional satisfaction.

REFERENCES CITED

Andre, F. 1934. Notes on the biology of *Oncopeltus fasciatus* (Dallas). Iowa State Coll. Jour. Sci. 9: 73–87.

Beck, S. D. 1953. Nutrition of the European corn borer, *Pyrausta nubilalis* (Hubn.). III. An unidentified dietary factor required for larval growth. Jour. Gen. Physiol. 36: 317–25.

Blatchley, W. S. 1926. Heteroptera of eastern North America. Indianapolis: Nature Publishing Co.

Carter, W. 1927. A technic for use with homopterous vectors of plant disease, with special reference to the sugar-beet leafhopper, *Eutettix tenellus* (Baker). Jour. Agric. Res. 34: 449–51.

Frings, H., M. Frings, and F. Little. 1957. Peanuts as substitute food for the large milkweed bug. Jour. Econ. Ent. 50: 363–64.

Frings, H., and L. Peissner. 1952. Substitutes for milkweed seeds in the rearing of milkweed bugs. Jour. Econ. Ent. 45: 752.

Hamilton, M. A. 1935. Further experiments on the artificial feeding of *Myzus persicae* (Sulz.). Ann. Appl. Biol. 22: 243–58.

Hussey, R. F. 1952. Food plants and new records for some Hemiptera in Florida. Florida Ent. 35: 117–18.

Lea, A. O., and R. E. Neiswander. 1950. *Oncopeltus fasciatus* reared for laboratory testing on watermelon seeds. Jour. Econ. Ent. 43: 386.

Maltais, J. B. 1952. A simple apparatus for feeding aphids aseptically on chemically defined diets. Canadian Ent. 84: 291–92.

Scheel, C. A., S. D. Beck, and J. T. Medler. 1957. Nutrition of plant-sucking Hemiptera. Science 125: 444–45.

THE GENUS EUARESTOIDES IN THE UNITED STATES AND MEXICO (DIPTERA, TEPHRITIDAE)[1]

RICHARD H. FOOTE

Entomology Research Division, Agr. Res. Serv., U. S. D. A.

ABSTRACT

Examination of the types of *E. abstersa* (Loew, 1862) and *E. acutangula* (Thomson, 1868) shows these to be distinct species. Specimens of *abstersa* have been seen only from the Atlantic States, from New York to Florida, while *acutangula* is known to range from the Pacific States eastward at least to Minnesota and Indiana. *E.* **arnaudi** from California and *E.* **dreisbachi** from Mexico are included in a key to the four species now known in the genus.

The present study was undertaken to resolve a long-standing confusion in the identity and distribution of two common North American fruit flies and to place them, together with two new species, in a suitable generic position.

Trypeta abstersa Loew, 1862, was described from material in the Winthem collection, collected in "Amérique septentrionale". In 1868, C. G. Thomson described *Trypeta acutangula* from material collected in California. In one of his important papers on American fruit flies, Loew (1873) placed *acutangula* in *Tephritis*, a group known to him by a number of species that now properly belong to four or more genera; at the

[1]Accepted for publication December 27, 1957.

same time he placed *abstersa* in *Urellia*, believing it to be more closely related to members of the genus *Trupanea*.

For a number of years *acutangula* was assumed to be conspecific with *abstersa*. This was due in part to the fact that Loew's description of *abstersa* in English was readily available and that his figure of the wing of that species might well conform to Thomson's description, and in part to the relatively difficult translation of Thomson's original description of *acutangula* from the Latin and lack of illustrations in Thomson's work.

which are constant in large series from various localities, a discovery which supports beyond doubt the fact that they are indeed distinct species. The accompanying map (fig. 1) indicates that *abstersa*, previously thought to occur throughout the United States, is apparently restricted to the States bordering the Atlantic Ocean, and that *acutangula*, the identity of which has been in doubt for a number of years, is far more extensively distributed.

This new concept of the distribution of *abstersa* and *acutangula* indicates the necessity for a re-examination of the use of these names in

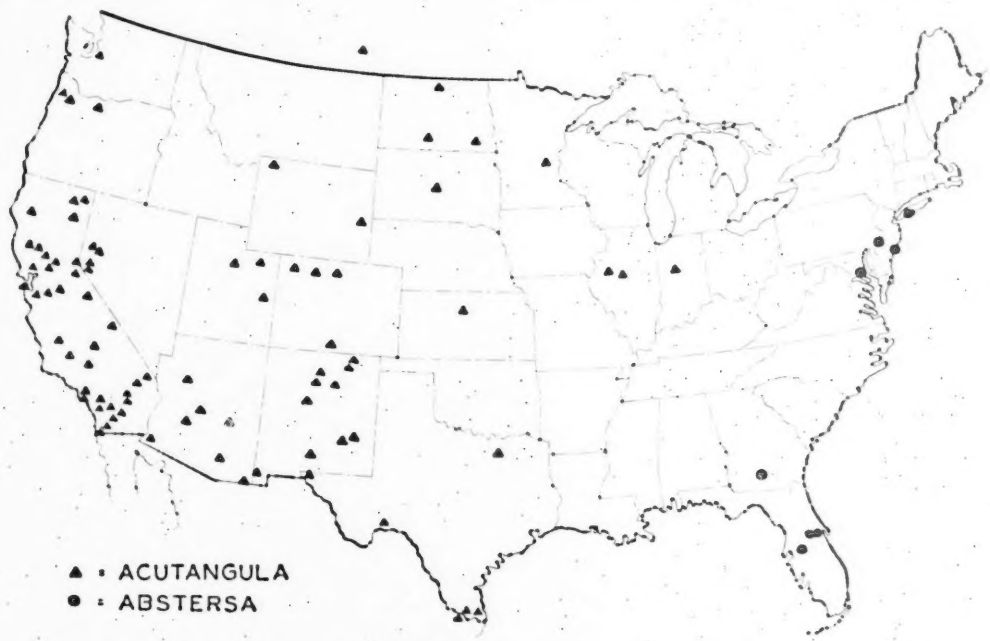


FIG. 1.—Distribution of *Euarestoides acutangula* and *E. abstersa* based on specimens examined in this study.

E. abstersa has been placed by various authors in *Trypeta*, *Urellia*, *Trypanea*, *Euaresta* and *Neotephritis*. In 1934 Benjamin erected *Euarestoides*, a new subgenus of *Neotephritis*, for this species to indicate its close relationship to *Neotephritis finalis* (Loew), a larger species with similar chaetotaxy but with a markedly different wing pattern. Hering (1941) later raised *Euarestoides* to full generic rank, with *abstersa*, *acutangula*, and a third species, *eugenia* van der Wulp; the last-named I believe to be a *Trupanea*. As presently defined, *Euaresta* and *Trupanea* exclude the four species treated here; because the genus *Neotephritis* contains a number of closely related species that have a quite different habitus, I concur with Hering (1941) and Quisenberry (1951) that *Euarestoides* is entitled to full generic status.

The types of the two species, borrowed from European museums for study, reveal differences

several widely used publications. Unfortunately, references to these cannot be included in the respective synonymies because the information given in them is too scanty to permit specific identification, and I have not had an opportunity to examine specimens upon which these records were based. They are as follows:

Loew, 1873, Smithsonian Misc. Coll. No. 256: 323, Observation 1 (*Trypeta abstersa:* I have not seen any Cuban tephritids assignable to *Euarestoides*, and the identification here must remain tentative); Wulp, 1900, Biol. Cent.-Amer., Diptera, 2: 426 (*Urellia abstersa:* Mexico City record probably another species); Aldrich, 1905, Smithsonian Misc. Coll. No. 1444: 611, 613 (*Urellia abstersa, Tephritis acutangula:* New Jersey and Key West records probably *abstersa*, remainder *acutangula*); Hendel, 1914 (1912), Abhandl. u. Ber. Dresden

14: 81 (*Trypanea abstersa;* description fits neither *abstersa* nor *acutangula);* Phillips, 1923, Jour. New York Ent. Soc. 38: 148, fig. 60 (*Trypanea abstersa;* New York specimens probably *abstersa,* remainder *acutangula,* as is the wing figure); Curran, 1932, Amer. Mus. Novitates No. 556: 6 (*Trypanea abstersa;* source of information not given); Aczél, 1949, Acta Zool. Lilloana 7: 292, 293 (*Euarestoides abstersa, E. acutangula; abstersa* is a mixed entry here; *acutangula* a misidentification); Aczél, 1951, Acta Zool. Lilloana 12: 130 (*Euarestoides abstersa;* probably an incorrect entry referring to some other species.

The total number of specimens examined and the dates of collection from each state are summarized in the discussion for each species; discrete localities are shown only approximately by the map for *abstersa* and *acutangula* but are listed in detail for the new species. "Host" data have been taken from labels pinned with specimens and do not necessarily reflect true hosts.

I gratefully acknowledge the assistance of the following persons and institutions in allowing me to examine their collections: A. T. McClay, University of California at Davis (UCD); F. L. Blanc, California State Department of Agriculture, Sacramento; E. S. Ross, California Academy of Sciences, San Francisco (CAS); George Wallace, Carnegie Museum, Pittsburg, Pa. (CM); Paul H. Arnaud, Jr., formerly at Stanford University, Calif. (PHA); and R. R. Dreisbach, Midland, Mich. (RRD). I also wish to thank M. Beier, Naturhistorisches Museum, Vienna, for the loan of the holotype of *Trypeta abstersa,* and the Director, Naturhistoriske Riksmuseum, Stockholm, for sending the holotype of *Trypeta acutangula* for study. The present locations of paratypes of the new species herein described are designated by the codes entered in parentheses above.

Genus **Euarestoides** Benjamin

Trupanea (*Euarestoides*) Benjamin, 1934, U. S. D. A. Tech. Bull. 401: 57 (type: *Trypeta abstersa* Lw.; *T. acutangula* Thoms. also included).

Euarestoides; Hering, 1941, Beitr. Fauna Perus 1: 164 (first to raise to full generic rank); Quisenberry, 1951, Jour. Kansas Ent. Soc. 24: 59 (accepts Hering's conclusions); Aczél, 1951, Acta Zool. Lilloana 12: 130 (corrects misspelling in 1949 reference).

Eurestoide; Aczél, 1949, Acta Zool. Lilloana 7: 292 (*abstersa* and *acutangula* included, with respective synonymies).

DIAGNOSIS.—Anterior oral margin normal, not strongly produced; eye suboval; proboscis normal, not distinctly geniculate; two pairs upper frontoorbitals, the posterior pair erect, not convergent; three pairs lower frontoorbitals. Wing with the brown, pre-apical dark area as in *Trupanea;* in addition, proximal half occupied by a yellowish or light brown reticulate pattern; R_{4+5} bare. Humerals and supraalars present; no presutural dorsocentrals; postsutural dorsocentrals nearer to transverse suture than to a transverse line between the supraalars; acrostichals nearer to scutellum than to a transverse line between the wing bases; two pairs well developed scutellars.

All members of the genus may be quickly recognized by the characteristic wing pattern (figs. 6–9) consisting of a yellow or brown reticulation in the proximal half and a dark brown preapical area such as that possessed by species of *Trupanea,* and by the presence of three pairs of lower frontoorbitals.

KEY TO THE SPECIES OF *EUARESTOIDES*

1. Wing pattern (Fig. 7) the same brown color throughout, the pattern in proximal half fainter than in distal half but not distinctly yellow . . . . . **acutangula** (Thoms.)
   Pattern in proximal half of wing distinctly yellowish in contrast to the dark brown of distal half, the line of demarcation rather abrupt 2
2. Dark area in distal half of cell R_1 with a small hyaline spot close to its center (Fig. 6) . . . **abstersa** (Loew)
   This dark area with the hyaline spot distinctly closer to the termination of vein R_{4+5} than to the center . 3
3. Proximal half of subcostal cell, cell R_1 directly below subcostal cell, proximal half of cell R_5, and almost all of cell R distinctly yellow, with few or no indications of hyaline spots (Fig. 8); ovipositor sheath glistening black . . . . . **arnaudi**, new species
   This area with numerous hyaline spots, especially in cell R and proximal half of cell R_5 (Fig. 9); ovipositor sheath uniform yellowish brown . . . . . **dreisbachi**, new species

Euarestoides abstersa (Loew)

(Figs. 2, 6)

Trypeta abstersa Loew, 1862, Berlin. Ent. Zeitschr. 6: 221 (Centuria II, p. 91); Loew, 1873, Smithsonian Misc. Coll. 11(256): 322, Pl. XI, fig. 7 (the figure and description undoubtedly *abstersa*).

Urellia abstersa; Loew, 1873, Smithsonian Misc. Coll. 11(256): 329; Johnson, 1895, Proc. Acad. Nat. Sci. Philadelphia, Sept. 1895: 337 (I have examined the specimen upon which this reference is based); Adams, 1904, Kansas Univ. Sci. Bull. 2(14): 450; Johnson, 1909, Psyche 16: 113; Johnson, 1910, Ann. Rept. New Jersey State Mus. for 1909: 803; Johnson, 1913, Bull. Amer. Mus. Nat. Hist. 32: 84 (I have seen at least one of these specimens).

Trypeta (*Urellia*) *abstersa*; Osten Sacken, 1878, Smithsonian Misc. Coll. 16(270): 194 (cites Loew's 1873 records).

Euaresta abstersa; Coquillett, 1899, Jour. New York Ent. Soc. 7: 265 (incorrectly synonymizes *acutangula*).

Trypanea abstersa; Johnson, 1925, Occas. Papers Boston Soc. Nat. Hist. 7: 264; Leonard, 1928, Cornell Univ. Agric. Expt. Sta. Mem. 101: 853.

Trupanea (*Euarestoides*) *abstersa*; Benjamin, 1934, U. S. Dept. Agric. Tech. Bull. 401: 58, fig. 43, A-I. (I have seen Benjamin's Florida material).

Euarestoides abstersa; Hering, 1941, Beitr. Fauna Perus 1: 165; Quisenberry, 1951, Jour. Kansas Ent. Soc. 24: 59 (accepts Hering's generic placement and *acutangula* as a separate species).

SPECIMENS EXAMINED.—Holotype ♀, bearing the labels "Am. sept.", "Coll. Winthem", "84", "abstersa, det. Loew", deposited in the Naturhistorisches Museum, Vienna. FLORIDA: 11 ♂♂, 11 ♀♀, 12 November-17 December, 1929. GEORGIA: 1 ♂, (So. Georgia—no other data). MARYLAND: 3 ♂♂, 4 ♀♀, 12 July-12 October, 1925–1931. NEW JERSEY: 3 ♂♂, 3 ♀♀, 13 June-2 October, 1909–1935. NEW YORK: 1 ♀, 21 October, 1935.

HOSTS.—*Solidago* sp., *Trilisa paniculata*, flowers of "seablite".

REMARKS.—In addition to the characters presented in the key, *abstersa* may be recognized by the faint but discrete spots in the proximal yellowish half of the wing (fig. 6); by the distinct but narrow extensions of the pre-apical dark spot, one proximally bordering the hyaline spot which is located immediately anterior to the m-cu crossvein, the other extending from the apex of the subcostal cell to a point on vein R_{4+5} opposite the m-cu crossvein; and by the apex of cell R_5, which contains a hyaline spot that is wider than long. The ovipositor sheath is entirely yellow. As far as known, this species is restricted to the Atlantic States (fig. 1); its limit of distribution westward is not known.

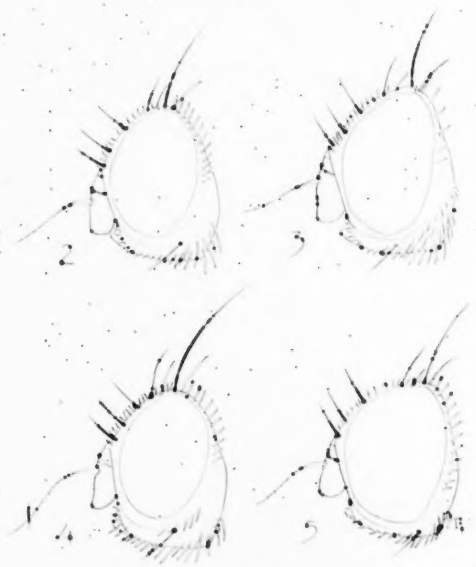


FIG. 2.—*Euarestoides abstersa* (Loew), lateral view of ♀ head.
FIG. 3.—*Euarestoides acutangula* (Thoms.), lateral view of ♀ head.
FIG. 4.—*Euarestoides arnaudi*, new species, lateral view of head of holotype ♀.
FIG. 5.—*Euarestoides dreisbachi*, new species, lateral view of head of holotype ♀.

Euarestoides acutangula (Thomson)

(Figs. 3, 7)

Trypeta acutangula Thomson, 1868, Eugenies Resa Ins. 6(2): 583 (in Latin); Loew, 1873, Smithsonian Misc. Coll. 11(256): 342 (Thomson's original description reprinted).

Trypeta (*Urellia*) *acutangula*: Osten Sacken, 1878, Smithsonian Misc. Coll. 16(270): 194.

Urellia abstersa: Doane (misdet.), 1899, Jour. New York Ent. Soc. 7: 192; Snow (misdet.), 1903, Kansas Univ. Sci. Bull. 2(5): 219; Snow (misdet.), 1904, *ibid.* 2(12): 345.

Euaresta abstersa: Johnson (misdet.), 1903, Trans. Amer. Ent. Soc. 29: 106 (I have seen the Skinner-collected specimens); Cresson (misdet.), 1907, Trans. Amer. Ent. Soc. 33: 106.

Trupanea (*Euarestoides*) *acutangula*: Benjamin, 1934, U. S. Dept. Agric. Tech. Bull. 401: 58.

Euarestoides acutangula: Hering, 1941, Beitr. Fauna Peru 1: 165; Quisenberry, 1951, Jour. Kansas Ent. Soc. 24: 59.

SPECIMENS EXAMINED.—Holotype ♂, bearing the white labels "California", "Kimb.", "Typus", "Trypeta acutangula Thoms.", and the red label "74, 56". One additional ♂ with the same data but with neither the label "typus" nor the red label. Both deposited in the Naturhistoriske Riksmuseum, Stockholm. ARIZONA: 10♂♂, 16♀♀, 17 January-30 August, 1903–1955. CALIFORNIA: 176♂♂, 195♀♀, 11 January-24 November, 1915–1956. COLORADO: 6♂♂, 9♀♀, 11 June-3 August, 1906–1956. IDAHO: 1♀, 3 September, 1925. ILLINOIS: 1♀, 20 May, 1918. INDIANA: 2♂♂, 1♀, 28 April-22 May (no year). IOWA: 1♂, 25 September, 1889. MINNESOTA: 1♂ (no data). NEVADA: 3♂♂, 6♀♀, 14 February-6 July, 1911–1952. NEW MEXICO: 8♂♂, 10♀♀, 17 April-30 August, 1895–1955. NORTH DAKOTA: 3♀♀, 14–20 June, 1918. OREGON: 4♂♂, 3♀♀, 27 June-18 August, 1920–1947. SOUTH DAKOTA: 5♂♂, 28 October, 1915. TEXAS: 4♂♂, 5♀♀, 9 March-22 September, 1902–1945. UTAH: 10♂♂, 7♀♀, June-27 September, 1911–1953. WASHINGTON: 4♂♂, 1♀, 8 July, 1948. WYOMING: 2♀♀, 12 March-July, 1895–1907. CANADA: 1♂, 3♀♀, Medicine Hat (Alberta), October, 1911. MEXICO: 1♀, Laguna Madre, 25 mi. SE Harlingen, Texas (Tamaulipas), 30 January, 1945.

HOSTS.—Alfalfa, asparagus, chokecherry, *Chrysanthemum paniculatus*, *Franseria chaenopodifolia*, *Franseria villosa*, *G. sarothrae*, *Gaillardia aristata* (reared), *Hymenoclea salsola*, rice, *Senecio douglasi*, *Sesuvium sessile*, *Sisymbrium*, *Solidago canadensis arizonica* flrs., *Sphaeralcea angustifolia*, *Xanthium canadense*, *Xanthium* sp. flowers. It has also been taken at light, and in traps baited for melon fly.

REMARKS.—*E. acutangula* is the only species in the genus whose wing pattern (fig. 7) is wholly brown. Even though the markings in the proximal half of the wing tend to fade, there is no contrasting yellow color present. Furthermore, it is the only species in which the hyaline spots in the proximal half of the wing tend to coalesce so that the faded brown markings run irregular courses across the wing disc instead of forming a network. In contrast to all other species, the proximal third and the extreme tip of the ovipositor sheath is black, the remainder yellow, and the third antennal segment tends to darken (fig. 3). As indicated by the map (fig. 1) and distributional information given above, *acutangula* is by far the most widespread species of *Euarestoides* in North America. The eastern limit of its range in the United States is not known with certainty.

Euarestoides arnaudi, new species

(Figs. 4, 8)

Easily recognized by the distinctive unbroken

expanse of yellow in the anterior proximal half of the wing and by the pale and relatively short apical scutellars.

FEMALE.—*Head* (fig. 4): Entirely yellow, front 1.2 times as wide as one eye, nearly as wide at vertex as at lunule, with 25 to 35 short stout yellow hairs scattered over surface, each about the same length as those on first antennal segment; eye suboval; 3 brownish yellow lower frontoorbitals, the anterior pair shorter than the two subequal posterior pairs; posterior upper frontoorbital yellow, 0.75 times as long as brownish yellow anterior upper frontoorbital; brownish yellow inner vertical very long, 4 times as long as yellow outer vertical; all postocular setae yellow. Antenna and basal segment of arista yellow, terminal portion of arista brownish yellow. *Thorax*: With black ground color almost completely obscured by dense yellow pollinosity, covered with short, stout yellow bristles whose bases are closer together than the average bristle length. Proximal half of scutellum yellow in ground color, covered with yellow pollinosity, apex covered by hairs similar in color and length to those on disc of thorax; brownish yellow proximal scutellars about 3 times as long as apical scutellars. *Legs*: Entirely yellow. *Wing* (fig. 8): A dark brown area ("preapical spot" of authors) occupying distal third of cell R_1, the central portion of distal half of cell R_5, and the central half of cell R_5, with a small, inconspicuous bulla, and with narrow dark rays as follows: from r-m crossvein to apex of subcostal cell; from a point on vein R_{2+3} distad of r-m crossvein to costa and parallel with the first; 3 rays extending from center of cell R_5, one to costa halfway between the terminations of veins R_{2+3} and R_{4+5}, one to the termination of vein R_{4+5}, and one to the termination of vein M_{1+2}; 3 additional rays extending from the posterior border of the preapical spot to the posterior wing margin, one along the m-cu crossvein and two equally dividing second cell M_2. In addition, a rounded hyaline spot anterior to m-cu crossvein extending two-thirds of the distance across cell R_5, bounded proximally by a short, narrow dark brown ray from preapical spot, leaving a small, ill-defined but distinctly hyaline spot in antero-basal corner of cell R_5, and a small hyaline spot invading cell R_1 close to the termination of vein R_{2+3}. Subcostal cell, proximal half of cell R_1, all of cell R and all of those cells posterior to it with a yellow infuscation that contrasts strongly with the dark brown of preapical spot, a suggestion of one small hyaline spot near base of cell R_5 below stigma and one just posterior to it near middle of cell R. First cell M_2, cell Cu_1, and second anal cell occupied by ill-defined yellowish hyaline spots. *Abdomen*: Similar to thorax in color, pollinosity and setation; ovipositor sheath shiny black, covered with short, stout yellow hairs similar to those on abdomen, about 1.5 times as long as last two abdominal tergites together.

Male.—Similar to female in size, coloration and wing pattern; last visible abdominal tergite 1.8 to 2.0 times as long as the two preceding tergites together.

Holotype.—♀, Canada Road behind Belmont, San Mateo Co., Calif., 21.IX.52, swept from *Baccharis pilularis*, P. H. Arnaud. USNM Type No. 63546.

Paratypes.—2♂♂, same data as holotype (1♂ USNM, 1♂ PHA); 2♀♀, 1♂, Stanford

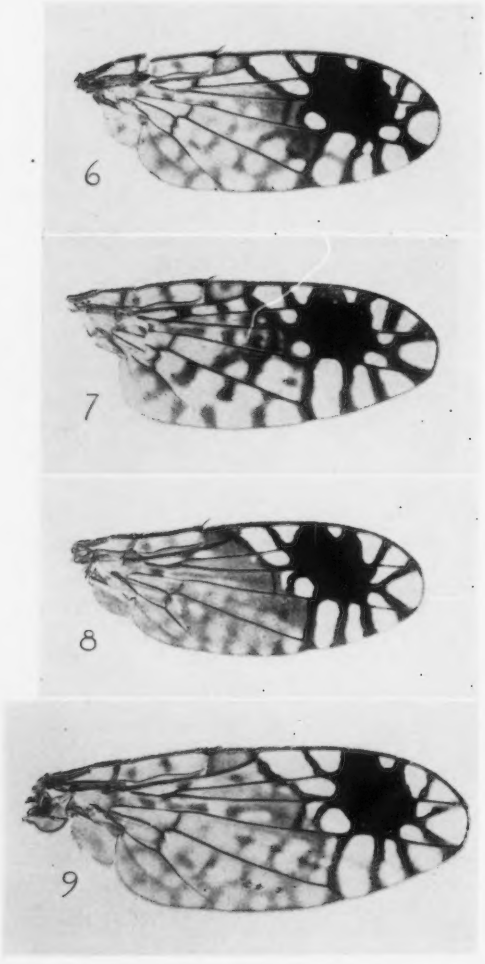


FIG. 6.—*Euarestoides abstersa* (Loew), right wing, ♂, Riverton, N. J.

FIG. 7.—*Euarestoides acutangula* (Thoms.), right wing, ♂, Burlington, Ore.

FIG. 8.—*Euarestoides arnaudi*, new species, right wing, paratype ♂, type locality.

FIG. 9.—*Euarestoides dreisbachi*, new species, right wing, paratype ♂, type locality.

University, Santa Clara Co., Calif., 27.X.52, P. H. Arnaud (1 ♀ USNM; 1 ♂, 1 ♀, PHA); 1 ♂, 1 ♀, 6 m. N. Klamath, Del Norte Co., Calif., 13.VIII.53, G. A. Marsh and R. O. Schuster (1 ♀, USNM; 1 ♂ UCD); 1 ♀, Mt. Hermon, Santa Cruz Co., Calif., 19.VII.22, F. E. Blaisdell (CAS); 1 ♂, San Francisco, Calif., 7.I.52, C. E. Kaufeldt (UCD).

Remarks.—I take pleasure in applying the patronym to express my high esteem for Paul H. Arnaud, Jr., and his work in the Diptera.

Euarestoides dreisbachi, new species

(Figs. 5, 9)

Distinguishable from *acutangula* by the yellow color in the proximal half of the wing; from *arnaudi*, new species, by the presence of hyaline spots in this yellow area; and from *abstersa* by the distal location of the small, hyaline costal spot in the apical half of cell R_1.

Female.—*Head* (fig. 5): Entirely yellow; width of frons at vertex equal to width of one eye; about the same width at vertex as at lunule, with 20 to 25 short, stout, yellow hairs scattered over surface, each about the same length as those on first antennal segment; eye suboval; 3 pairs brownish yellow lower frontoorbitals, the anterior pair shorter than the two subequal posterior pairs; posterior upper frontoorbital yellow, 0.6 times as long as brownish yellow anterior upper frontoorbital; brownish yellow inner vertical long, 3 times as long as yellow outer vertical; all postocular setae yellow. Antenna yellow; basal fourth of arista slightly expanded and yellow, terminal three-fourths of arista dark brown. *Thorax*: Black ground color almost completely obscured by dense yellow pollinosity; covered with short, stout, yellow setae whose bases are closer together than the average bristle length. Scutellum with yellow ground color covered with dense yellow pollinosity; beset with setae similar to those on disc of thorax. Brownish yellow apical scutellars 0.75 to 0.85 times as long as similarly colored proximal scutellars, the latter about 1.2 times as long as dorsocentrals. *Legs*: Wholly yellow. *Wing* (fig. 9): Pattern consisting of a dark brown area ("preapical spot" of authors) occupying distal third of cell R_1, the central portion of distal half of cell R_2, and the central half of cell R_3; without a bulla; this dark area with narrow dark brown rays as follows: from r-m crossvein to apex of subcostal cell; from a point on vein R_{2+3} distad of r-m crossvein to costa and parallel to first; 3 rays extending from the center of cell R_3, one to costa halfway between termination of veins R_{2+3} and R_{1+3}, one to the termination of vein R_{1+3}; 3 additional rays extending from the posterior edge of the preapical spot to the posterior margin of the wing, one lying on the m-cu crossvein, and 2 equally dividing second cell M_2. In addition, a hyaline spot anterior to m-cu crossvein extending at least three-fourths the distance across cell R_3, bounded proximally by a short, narrow dark brown ray from preapical spot, leaving a small, ill-defined but distinctly hyaline spot in the antero-basal corner of cell R_3; and a small hyaline spot invading cell R_1 close to termination of vein R_{2+3}. Subcostal cell, proximal half of cell R_1, all of cells R, M, first M_2, Cu_1, first and second anal cells yellow, contrasting with the dark brown of preapical spot, interrupted in all this area (except subcostal cell) by rather ill-defined hyaline spots, especially in cell R, in which these spots are subequal in size and equally spaced. *Abdomen*: Similar to thorax in color, pollinosity and setation, although there is a row of longer yellow setae along the posterior margin of each tergite; ovipositor sheath shining yellow, covered, but not as densely as abdomen, with short stout yellow setae, distinctly longer than 2 times the combined width of the two posteriormost tergites.

Male.—Similar to female in size, coloration and wing pattern; last visible abdominal tergite 2.0 times as long as combined widths of the two preceding tergites.

Holotype.—♀, La Primavera, Jalisco, Mexico, 7/8/56, R. & K. Dreisbach. USNM Type No. 63547.

Paratypes.—1 ♀, 6 ♂♂, same data as holotype (1 ♀, 2 ♂♂ USNM; 4 ♂♂, RRD); 1 ♀, Lagos de Morena, Mex., 6300', 8.12.54, R. R. Dreisbach (USNM); 1 ♂, 5 mi. N. Salamanca, Mex., 6000', R. R. Dreisbach (RRD); 2 ♀♀, 15 km. E. Sombrete, Zacatecas, Mex., 30.VII.51, P. D. Hurd (1 ♀ USNM; 1 ♀ UCD); 1 ♀, Lagunilla, Hidalgo, Mex., 14.VI.54, P. D. Hurd (UCD); 1 ♂, San Juan del Rio, Durango, Mex., 7.VIII.51, *Baccharis glutinosa*, P. D. Hurd (UCD); 1 ♂, Encarnacion de Diaz, Jalisco, Mex., 28.VII.51, P. D. Hurd (UCD); 1 ♀, 3 ♂♂, Guadalajara, Mex., McConnell 1909, H. Kahn Coll'n., C. M. Acc. No. 12676 (1 ♂ USNM; 1 ♀, 2 ♂♂, CM).

Remarks.—I have named this species for R. R. Dreisbach of Midland, Michigan, whose unusual interest in entomology has brought this new form to light.

REFERENCES CITED

Benjamin, F. H. 1934. Descriptions of some native trypetid flies with notes on their habits. U. S. Dept. Agric. Tech. Bull. 401: 1–95, 44 figs.

Hering, M. 1941. Trypetidae (Dipt.). Beitr. Fauna Perus 1: 121–76.

Loew, H. 1862. Diptera Americae septentrionalis indigena. Berlin. Ent. Zeitschr. 6: 185–232 (reprinted in Centuria II, pp. 55–102).

1873. Monographs of the Diptera of North America. Smithsonian Misc. Coll. 11(256): 1–347, Pls. VIII–XI.

Quisenberry, B. F. 1951. A study of the genus *Tephritis* Latreille in the Nearctic Region north of Mexico. Jour. Kansas Ent. Soc. 24: 56–72, 1 pl., 1 text fig.

Thomson, C. G. Kongliga Svenska Fregatten Eugenies resa omkring jorden. Insekter 6(2): 443–614, Pl. 9.

A PRELIMINARY STUDY ON FEEDING ORNITHODOROS SAVIGNYI (AUDOUIN) ON HUMAN BLOOD THROUGH ANIMAL-DERIVED MEMBRANES (ACARINA: ARGASIDAE)

I. BARRY TARSHIS

Department of Entomology, University of California, Los Angeles

ABSTRACT

An apparatus and a technique are described for *in vitro* feeding of this tick through animal-derived membranes on outdated, citrated, whole human blood. Mouse-skin and cottontail rabbit-skin membranes gave the highest feeding rates, 95.5% and 92.4% respectively. Membranes could be used a number of times without lowering the feeding rate of the ticks. Blood temperatures of 34°–35° C. and ambient temperatures of 26°–30° C. were found to be optimum for feeding ticks through membranes. The ticks fed equally well during morning and afternoon hours, and in light and dark rooms. Nymphs and adults, once established on the membranes, may become engorged in 5 and in 5 to 15 minutes respectively. Crowding by the ticks in the membrane chamber did not deter them from feeding. Coxal fluid was expelled copiously by fully engorged ticks approximately 1 to 5 minutes after the blood meal, and the fluid continued to flow intermittently for as long as 60 minutes. The presence of large quantities of coxal fluid within the membrane chamber did not deter feeding by the ticks.

The earliest work on an *in vitro* technique for feeding ticks was that done by Hindle and Merriman (1912). These workers, interested in the function of Haller's organ, removed tarsus I, on which this organ is located, of specimens of *Ornithodoros moubata* Murray, *Hyalomma aegyptium* (Linn.) and *Argus persicus* (Oken). After removal of the organ they successfully fed the ticks on a variety of solutions through membranes made from diaphragms and skins of rats. In 1933 Totze found that he could feed specimens of *Ixodes ricinus* L. and *Hyalomma marginatum brionicum* Schulze and Schlottke through cellophane membranes. Boné (1943), in his studies relating to the function of the coxal glands of *O. moubata*, was able to get these ticks to feed on normal guinea pig blood through mouse-skin membranes. In their studies of the nutritional requirements of *O. moubata*, DeMeillon and Golberg (1947) were able to get the ticks to feed through mouse-skin membranes on varying solutions.

A capillary tube method was developed by Chabaud (1950) for feeding the ixodid ticks *H. excavatum* Koch, *H. dromedarii* Koch, *Dermacentor pictus* Hermann and *Rhipicephalus sanguineus* (Latreille). A modification of this technique was used by Burgdorfer (1957) for infecting *D. andersoni* Stiles, and *Amblyomma maculatum* Koch with leptospira. Burgdorfer and Pickens (1954) successfully fed *O. moubata*, *O. turicata* (Duges), *O. parkeri* Cooley and *O. hermsi* Wheeler, Herms and Meyer on the air-sac membrane of infected embryonated eggs. Burgdorfer (1956) showed that adults and nymphs of *O. turicata* fed through air-sacs of embryonated eggs infected with leptospira could transmit the infection to susceptible guinea pigs. In his feeding experiments with *O. moubata*, Tarshis (1958) fed nymphs and adults of this species on heparinized beef blood through a variety of membranes, obtaining the best results (97 percent feeding) with juvenile New Zealand white rabbit-skin membranes.

The current paper reports on a number of membranes and an apparatus used for feeding *Ornithodoros savignyi* (Audouin) and results of experiments with the membranes and apparatus.

MATERIALS AND METHODS

Membrane Feeding Apparatus

The membrane feeding apparatus consists of (1) a thermostatically controlled water bath, (2) a chamber to hold the blood, and (3) a feeding chamber, to which a membrane is attached, to contain the ticks.

A 3-gallon, 9-inch-diameter, circular battery jar heated by a thermostatically controlled 40-watt aquarium immersion heater is used as a water bath.

The tick feeding chamber consists of (1) a plexiglas chamber to hold the ticks, (2) a plexiglas ring to secure the membrane to the tick chamber, (3) a plexiglas lid screened with 52 x 52 mesh saran screen cloth and (4) a plexiglas adaptor ring for holding the feeding chamber in an upright position in the blood chamber. After the membrane is secured to one open end of the tick chamber by the plexiglas ring, the excess membrane is trimmed away and the juncture of the chamber sides, the ring, and the edges of the membrane are covered with ½-inch wide waterproof plastic tape. This not only holds the membrane securely to the chamber but also insures against blood leaking into the cup.

The blood chamber is a ⅜-inch thick plexiglas cup, 4 inches in diameter and 3¼ inches deep. To form a support for the tick chamber adaptor ring, ⅛-inch of the inside surface of the top 2 inches of the blood chamber is trimmed away.

A ⅜-inch thick, 10-inch square waterproof plywood lid, with a 4-inch hole in the center for the blood chamber, fits on top of the water bath.

Two $\frac{3}{8}$-inch stainless steel, criss-crossed strips, attached to the under side of the lid, form a support $2\frac{1}{2}$ inches below the lid for the blood chamber. The plywood lid also has a $1\frac{1}{4}$-inch hole for insertion of the immersion heater. The construction details of the feeding apparatus and water bath are shown in figures 1, 2, and 3.

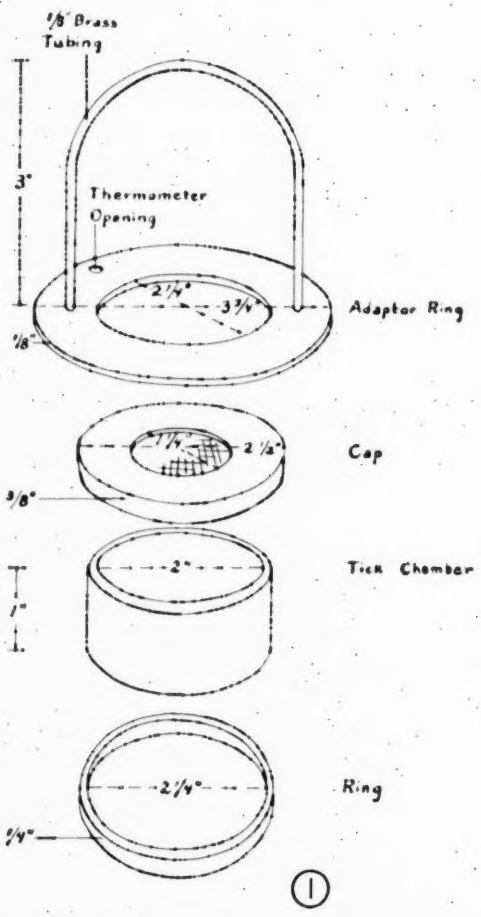
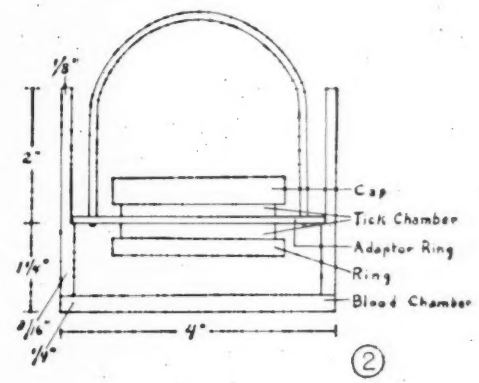


FIG. 1.—Membrane feeding chamber. All parts are of $\frac{1}{8}$-inch plexiglas except as otherwise specified. Polyethylene sealer is used to secure the 52 x 52 mesh Saran screen cloth to the cap. The brass handle is fastened to the adaptor ring from underneath with round-headed brass screws.

Membranes

The mouse-skin and cottontail rabbit-skin membranes were prepared from approximately 20- and 800-gram animals, respectively. The cottontail rabbits were shot in the wild and the mice were from laboratory colonies and were killed with chloroform. The fur from the animals was clipped with a pair of electric clippers until a very fine stubble was left. After removal from the animals the skins were stretched out and pinned fur side down onto a wooden board, and the heavy subcutaneous and fatty tissue removed. After this the skins were frozen for several hours, partially thawed, and then scraped with a blunt instrument until the fine tissue material was removed and a parchment-thin membrane obtained. Male animals are best since the mammillae of the females often leave holes in the



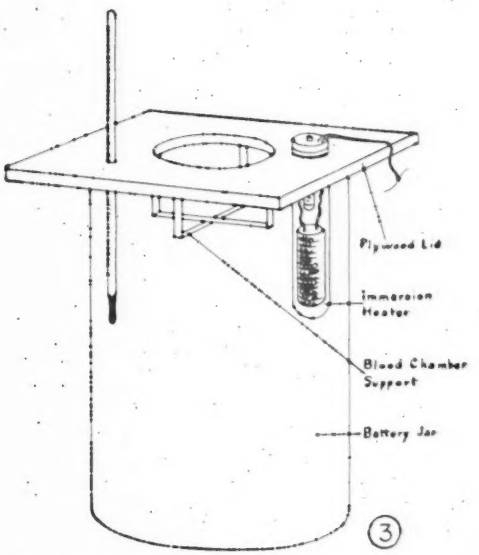


FIG. 2.—Section of plexiglas blood chamber showing placement of feeding apparatus on adaptor ring support within the blood chamber. The bottom of the chamber is sealed to the walls with polyethylene sealer. To form the adaptor ring support for the feeding apparatus, $\frac{1}{16}$ inch of the inside surface of the top 2 inches of the blood chamber is trimmed away.

FIG. 3.—Assembly of water bath showing construction details of lid and blood chamber support and placement of aquarium immersion heater in water bath.

skins after they are prepared. However, very small holes or tears of any kind can be repaired with collodion, clear nail polish or Ambroid's liquid cement, which are non-toxic to the ticks. The freshly prepared rodent skins need not be washed in water or alcohol prior to use.

FIG. 4.—Unfed (top), partially fed (center), and fully engorged (bottom) membrane-fed *Ornithodoros savignyi* (Audouin). Photo by Mr. Roy Pence.

Rodent-skin membranes may be prepared in advance and held in a frozen state for weeks or months. If desired, the subcutaneous and fatty tissue then may be left on for freezer storage and removed just prior to use. Since the skins have a tendency to become dry and leathery when frozen for a long period of time, it is advisable to soften them by floating on a surface of warm water for several minutes prior to placement on the blood. Ticks will feed as readily through previously frozen skins as they will through those freshly prepared.

"Silverlight" is prepared commercially from the outermost layer of the caecum of an ox and may be purchased from Julius Schmid, Inc., New York, N. Y. The "Nearkid" and "Zephir" membranes, prepared commercially from bovine intestines, and "Fourex," a prophylactic skin prepared commercially from the caecum of a lamb, also may be purchased from Julius Schmid, Inc. The Baudruche membranes are prepared commercially from bovine intestines by the Long and Long Company, Belleville, New Jersey.

Blood

Outdated, citrated whole human blood, obtained from the Clinical Laboratory, U.C.L.A. Medical Center, was used for feeding the ticks. The blood was stored in the original containers in a refrigerator held at 4° C. When needed, the blood was taken from the container, warmed to the desired temperature, and placed into the blood chamber of the feeding apparatus where a constant temperature was maintained throughout the feeding period.

TICKS

The ticks used in these experiments were nymphs and adults of *Ornithodoros savignyi* (Audouin) obtained from Harry Hoogstraal, Medical Zoology Department, Naval Medical Research Unit No. 3, Cairo, Egypt. All ticks were field-collected on October 10, 1957, and when received in our laboratory were flattened and appeared to have been completely unfed; this was further evidenced by their readiness to ingest blood through membranes during the current feeding experiments. The ticks were held at a temperature of 26° C. with a relative humidity of approximately 35 percent prior to being fed through the membranes.

Just prior to feeding, the ticks were stimulated with light and a little heat and then the active ticks only were selected and placed into the feeding chamber. The chamber was then placed on the blood and the ticks were allowed to feed undisturbed for varying periods of time.

At the conclusion of each feeding experiment, the feeding chamber was removed from the blood, the excess blood washed from the bottom of the chamber and the membrane, and the ticks removed for determination of the number that had fed.

Body shape was used to determine whether or not, and how much, ticks had fed; ticks with only slightly distended bodies were tabulated as partially fed and those with fully distended bodies as fully engorged (Fig. 4). The only way to determine whether the more flattened ticks took in any blood was to crush them. This was done with only a few ticks, since it was desirable to keep most of the ticks alive whether they had

fed or not. Most of the crushed ticks contained freshly ingested blood; therefore, since the feeding rates reported here are those for only partially and fully engorged ticks, it is likely that they are somewhat lower than actually was the case. However, since the greatest number of ticks fed sufficiently to be tabulated as fed, this possible discrepancy is not too significant.

In placing the membrane chamber on the blood, care should be taken that the membrane across the bottom of the chamber is completely covered with blood and slightly submerged in the blood, so as to leave no air spaces between the blood and membrane. The membrane should be placed somewhat loosely on the cup so that when the blood comes in contact with the membrane it will push the membrane up to form a very slight bleb, or dome. The bleb should not be too high or the ticks will slide down the sides of it. The purpose of the bleb is to create a slight degree of pressure, which enables the ticks to feed better.

RESULTS AND DISCUSSION

Blood temperatures ranging from 36° to 45° C. have been used by various investigators employing membrane feeding methods for haematophagous arthropods (Bishop and Gilchrist, 1946; DeMeillon *et al.*, 1948; Fuller *et al.*, 1949; Trembley, 1952; Kartman, 1954; Haddon, 1956). The author (1958) found that he could obtain high feeding rates with fleas, ticks and mosquitoes fed through various membranes on blood maintained at approximately 34° C. In the current experiments *O. savignyi* also fed well on blood held between 34° and 35° C.

Haddon (1956) found that the human body louse fed best when the ambient temperatures were 26° to 30° C. Similarly, Tarshis (1958) found that ambient temperatures between 19° and 30° C. yielded high feeding rates for fleas, ticks, and mosquitoes. In feeding *O. savignyi* during the current investigation high feeding rates were obtained when the ambient temperature was between 25° and 30° C.

TABLE I

RESULTS OF FEEDING *O. savignyi* (AUBOUIN) ON OUTDATED, CITRATED WHOLE HUMAN BLOOD THROUGH 11 DIFFERENT ANIMAL DERIVED MEMBRANES

Membrane	Exposure Time (Minutes)	Stage Exposed	Total No. Used	Number Examined			Total Number Fed	Percent Fed of Total Used	Percent Engorged of Total Fed
				Unfed	Fed				
					Partially	Fully Engorged			
Mouse skin	45	Nymphs	88	4	19	65	84	95.5	77.4
Rabbit skin	30-60	Nymphs Adults	170	13	23	134	157	92.4	85.4
Nearkid	60-180	Nymphs Adults	183	112	10	61	71	38.8	85.9
Zephir	60-180	Nymphs Adults	57	43	6	8	14	24.6	57.1
Baudruche									
Transparent	45	Nymphs	20	18	1	1	2	10.0	50.0
Black	45	Nymphs	61	57	0	4	4	6.6	100.0
Fourex	45-180	Nymphs Adults	79	74	2	3	5	6.3	60.0
Baudruche									
Yellow	45	Nymphs	47	46	0	1	1	2.1	100.0
Purple	45	Nymphs	45	45	0	0	0	0	0
Blue	45	Nymphs	55	55	0	0	0	0	0
Silverlight	45-180	Nymphs Adults	36	36	0	0	0	0	0

Ticks were unfed, field collected, and of unknown age.
Blood maintained at approximately 34.5° C., ambient temperature 25.5°-29° C.

Of 11 animal-derived membranes screened in the current studies (Table I), cottontail rabbit-skin and mouse-skin membranes gave the highest feeding rates, 92.4 and 95.5 percent, respectively. Nearkid and Zephir gave the next highest feeding rates, 38.8 and 24.6 percent, respectively.

Though Kartman (1954) and Tarshis (1958) showed that thin membranes gave the highest feeding rates for fleas and mosquitoes, results obtained in the current studies indicate that membrane thinness is not a vital factor in tick feeding. The highest tick-feeding rates were obtained with comparatively thick rodent-skin membranes rather than the thinner commercially prepared membranes (Nearkid, Zephir and Baud-

ruche). Tarshis (1958) found that membranes prepared from the skins of New Zealand white rabbits yielded exceedingly high feeding rates with *O. moubata* also.

Ticks fed during the morning and afternoon hours yielded approximately the same feeding results with each membrane used. There was also no effect on feeding by the ticks when the room was darkened.

Results of feeding nymphs of *O. savignyi* through cottontail rabbit-skin membranes for varying periods of time (Table II) showed that those ticks fed best that were left in the feeding chambers from 45 to 60 minutes. Ticks rarely will commence to feed within the first 5 minutes after being placed into the membrane feeding chamber, but as soon as they do settle down on the membrane surface and become attached, feeding commences and they may become completely engorged in as little as 5 minutes. Since feeding is the longest (average 26, minimum 17, maximum 53 minutes). The average male feeding is 16 minutes (minimum 9, maximum 42) and female 35 minutes (minimum 21, maximum 72).

It was found that membranes could be used several times without lowering the feeding rates of the ticks. After each feeding experiment, the membrane and membrane chamber should be washed and air dried. The assembled membrane feeding chambers can be stored in a 4° C. refrigerator overnight or longer. Tarshis (1958) found that fleas, *Xenopsylla cheopis* (Roth.), also could be fed through membranes that had been used a number of times without decreasing the feeding rates by the fleas.

Crowding by the ticks in the 2-inch feeding chamber did not deter feeding. As many as 32 nymphs of *O. savignyi* fed to full engorgement at one time in this small chamber.

TABLE II

RESULTS OF FEEDING NYMPHS OF *Ornithodoros savignyi* (AUDOUIN) ON CITRATED, WHOLE HUMAN BLOOD THROUGH RABBIT SKIN MEMBRANES FOR VARYING PERIODS OF TIME

EXPOSURE TIME IN MEMBRANE CHAMBER (MINUTES)	TOTAL NUMBER USED	NUMBER EXAMINED			TOTAL NUMBER FED	PERCENT FED OF TOTAL USED	PERCENT ENGORGED OF TOTAL FED
		Unfed	Fed				
			Partially	Fully Engorged			
5	20	17	1	2	3	15 0	66 6
10	20	13	2	5	7	35 0	71 4
15	15	3	3	9	12	80 0	75 0
30	35	4	6	25	31	88 6	80 6
45	20	0	2	18	20	100 0	90 0
60	47	0	4	43	47	100 0	91 5

Ticks were unfed and field collected, and of unknown age.
Blood temperature 34°–35° C.
Ambient temperature 25°–26° C.

the highest feeding rates occurred in the 45- and 60-minute experiments it would seem that most of the ticks took approximately 40 to 55 minutes to settle down and commence feeding. Most of the ticks were completely engorged at the end of these exposure periods. Thus, it is important to allow the ticks to remain in the membrane chambers for periods of 45 to 60 minutes or more if all are to become engorged.

Adults of *O. savignyi* took from 5 to 15 minutes to become completely engorged once they settled down on the membrane surface and commenced to feed. The settling down period was between 30 and 50 minutes.

Lees (1946) and Hoogstraal (1956) report that species of *Ornithodoros* become engorged in 30 minutes. Jobling (1925) noted that first instar nymphs of *O. moubata* feed on the average of 25 minutes (minimum 13, maximum 87). Second and third instars average about 4 minutes less (minimum 11, maximum 54), while fourth-instar

Upon opening the tick feeding chamber at the termination of each feeding experiment, it was noted that the interior of the chamber was extremely moist. At first it was thought that this wet condition might be due to "sweating," but on closer examination it was noted that the fully engorged ticks were expelling copious quantities of coxal fluid. Further observations revealed that coxal fluid commences to flow from 1 to 5 minutes after the tick becomes fully engorged and detached, and it continues to flow intermittently for as long as 60 minutes. Lees (1946) noted that in *O. moubata* coxal fluid began to flow about 15 minutes after these ticks began to feed and continued quite profusely until the ticks became detached, and then off and on for an hour or so.

Regardless of the amount of coxal fluid within the feeding chambers, unfed and partially fed ticks continued to feed undisturbed. Therefore, the low feeding rates obtained with some mem-

branes was not due to coxal fluid within the membrane chamber but to other conditions.

REFERENCES CITED

Bishop, A., and **B. M. Gilchrist.** 1946. Experiments upon the feeding of *Aedes aegypti* through animal membranes with a view to applying this method to the chemotherapy of malaria. Parasitology 37: 85–100.

Boné, G. J. 1943. Recherches sur les glandes coxales et la régulation du milieu interne chez l'*Ornithodoros moubata* Murray (Acarina, Ixodidae). Ann. Soc. Roy. Zool. Belgique 74: 16–31.

Burgdorfer, W. 1956. The possible role of ticks as vectors of leptospirae. I. Transmission of *Leptospira pomona* by the argasid tick, *Ornithodoros turicata* and the persistence of this organism in its tissues. Exptl. Parasitol. 5: 571–9.

1957. Artificial feeding of ixodid ticks for studies on the transmission of disease agents. Jour. Infect. Dis. 100: 212–4.

Burgdorfer, W., and **E. C. Pickens.** 1954. A technique employing embryonated chicken eggs for the infection of argasid ticks with *Coxiella burnetii*, *Bacterium tularense*, *Leptospira icterohaemorrhagiae*, and western equine encephalitis virus. Jour. Infect. Dis. 94: 84–89.

Chabaud, A. G. 1950. Sur la nutrition artificielle de tiques. Ann. Parasitol. 25: 42–47.

DeMeillon, B., and **L. Golberg.** 1947. Preliminary studies on the nutritional requirements of the bedbug (*Cimex lectularius* L.) and the tick (*Ornithodoros moubata* Murray). Jour. Exptl. Biol. 24: 41–63.

DeMeillon, B., J. M. Thorp, and **F. Hardy.** 1948. An apparatus for the rapid screening of drugs for possible use in chemotherapeutic control of ectoparasites and some results obtained with it. S. African Jour. Med. Sci. 13: 115–20.

Fuller, H. S., E. S. Murray, and **J. C. Snyder.** 1949. Studies of human body lice. *Pediculus humanus corporis*. I. A method for feeding lice through membrane and experimental infection with *Rickettsia prowazeki*, *R. mooseri*, and *Borrelia novyi*. Publ. Health Repts. 64: 1287–92.

Haddon, W. 1956. An artificial membrane and apparatus for the feeding of the human body louse, *Pediculus humanus corporis*. Amer. Jour. Trop. Med. Hyg. 5: 315–25.

Hindle, E., and **G. Merriman.** 1912. The sensory perceptions of *Argas persicus* (Oken). Parasitology 5: 203–16.

Hoogstraal, H. 1956. African Ixodoidea. I. The ticks of the Sudan (with special reference to Equatoria Province and with preliminary reviews of the genera *Boophilus*, *Margaropus*, and *Hyalomma*). U. S. Naval Res. Rept. NM 005 050.29.07. 1101 pages.

Jobling, B. 1925. A contribution to the biology of *Ornithodoros moubata* Murray. Bull. Ent. Res. 15: 271–80.

Kartman, L. 1954. An apparatus for the artificial feeding of fleas. Exptl. Parasitol. 3: 525–37.

Lees, A. D. 1946. Chloride regulation and function of the coxal glands in ticks. Parasitology 37: 172–84.

Tarshis, I. B. 1958. Feeding techniques for blood-sucking arthropods. Proc. 10th Internatl. Congr. Ent. Montreal 1956 (in press).

Totze, R. 1933. Beiträge zur Sinnesphysiologie der Zecken. Zeitschr. vergl. Physiol. 19: 110–61.

Trembley, H. L. 1952. The distribution of certain liquids in the esophageal diverticula and stomach of mosquitoes. Amer. Jour. Trop. Med. Hyg. 1: 693–710.

VITAMIN REQUIREMENTS OF THE HOUSE FLY, MUSCA DOMESTICA L. (DIPTERA: MUSCIDAE)[1,2]

H. L. HOUSE AND J. S. BARLOW[3]

Entomology Laboratory, Belleville, Ontario

ABSTRACT

For every 100 house fly larvae placed on a chemically defined medium, 64 reached maturity, 56 pupated, and 27 adults emerged. Several second-generation larvae were obtained. Feeding tests showed that omission of riboflavin, calcium pantothenate, nicotinic acid, or biotin from the food resulted in significant mortality during the first instar, and of thiamin by the third instar. Omission of choline or pyridoxine did not affect larval survival but led to significant mortality at pupation. Therefore, these seven vitamins are considered dietary requirements of the larvae. No requirement for *p*-aminobenzoic acid, inositol, or folic acid was shown.

During the development of a chemically defined diet for *Pseudosarcophaga affinis* (Fall.) (House 1954a, b, c, d; House and Barlow 1956, 1957a), periodic attempts were made to rear house flies, *Musca domestica* L., aseptically on the same media. The medium and the aseptic technique described in this paper have generally produced about 20 adults per hundred larvae. Though satisfactory growth on this medium is still not achieved, the medium was used as a basis for determining the qualitative vitamin requirements of the house fly.

[1]Contribution No. 3721, Entomology Division, and No. 383, Chemistry Division, Science Service, Department of Agriculture, Ottawa, Canada. Accepted for publication January 20, 1958.

[2]The assistance of Miss C. M. Rutherford, Mr. G. A. Denyes, and Mr. R. R. Williams, Entomology Laboratory, Belleville, is gratefully acknowledged.

[3]Senior Entomologist and Associate Chemist, respectively.

MATERIALS AND METHODS

The house fly colony at the Belleville Laboratory was established from pupae of a 3-year-old colony maintained at the Science Service Laboratory, London, Ontario. The insects are maintained on Richardson's (1932) medium and

the adults are fed milk. The females oviposit on sour milk.

To obtain aseptic larvae an egg mass was shaken and stirred in soapy water to separate the eggs. These were transferred to a small gooch crucible and the soap was removed with several rinses of sterile distilled water. The eggs were then covered with a 2.5% solution of formaldehyde, which was drained away in 3 or 4 minutes, and was followed by several rinses in sterile distilled water to remove the residual formaldehyde. A sterile camel's-hair brush was used to transfer the eggs to a large sterile test tube that contained a strip of moist filter paper; here they were allowed to hatch at room temperature. Single sterile larvae were transferred aseptically to test tubes, ⅜ inch by 3 inches, each containing about 1 ml. of medium. The composition of the medium is shown in Table I.

The medium was made up as described for the *P. affinis* diet (House and Barlow 1956). The qualitative vitamin requirements of the insect were determined by removing the vitamins from the medium one at a time. The growth on each deficient medium was tested with four groups of approximately 50 larvae, and each group was compared with the growth of a similar number of larvae on the complete medium. The larvae were examined daily and the time in days for each larval instar at 22.5° C. was recorded. All dead 24 hours after transfer to the medium were presumed to have died as a result of manipulation, and all larvae on media that showed evidence of contamination with micro-organisms were disregarded in assessing the results.

Asepsis was broken 7 days after 50% of the larvae had reached the third instar and the larvae were then transferred to pupa containers and allowed to pupate and emerge, as described for *P. affinis* larvae (House and Barlow 1957b).

The significance of differences between the control and experimental groups was tested by *t* tests (Goulden 1939).

TABLE I

COMPOSITION OF MEDIUM FOR ASEPTIC REARING OF *Musca domestica* L.

CONSTITUENT	MG./ML. H_2O
L-Amino Acid Mixture	20 00
Alanine	1 00
Arginine-HCl	1 22
Aspartic acid	1 28
Cysteine-HCl	0 26
Glutamic acid	2 10
Glycine	1 56
Histidine-HCl	0 48
Hydroxyproline	0 34
Isoleucine	1 04
Leucine	1 54
Lysine	1 16
Methionine	0 60
Phenylalanine	1 34
Proline	1 50
Serine	1 34
Threonine	1 08
Tryptophane	0 28
Tryosine	0 70
Valine	1 18
Inorganic Salts (Mixture No. 2, U.S.P. XII)	0 66
Sodium chloride	0 0287
Magnesium sulphate	0 0904
Sodium biphosphate	0 0576
Potassium phosphate (K_2HPO_4)	0 1583
Calcium biphosphate ($CaH_4(PO_4)_2$)	0 0896
Ferric citrate (17.5% Fe)	0 0196
Calcium lactate	0 2157
Lipids	7 70
Cholesterol	1 00
Linoleic acid	0 60
Linolenic acid	0 20
Oleic acid	1 92
Palmitic acid	0 88
Stearic acid	0 40
Tween 80 (polyoxyethylene sorbitan monoleate, Atlas Powder Co., Ltd., of Canada, Brantford, Ont.)	2 70
B-Vitamins	
Biotin	9×10^{-5}
Calcium pantothenate	0 0044
Choline chloride	0 0200
Folic acid	0 0034
Inositol	0 0596
Nicotinic acid	0 0030
p-Aminobenzoic acid	0 0090
Pyridoxine-HCl	0 0090
Riboflavin	0 0016
Thiamine-HCl	0 0012
Miscellaneous	
Dextrose	5 0
Ribonucleic acid	0 75
Potassium hydroxide	2 47
Agar	15

RESULTS AND DISCUSSION

During the experiments 64% of a total of nearly 200 larvae placed on the complete medium reached maturity, 88% of these formed puparia, and adult flies emerged from 48% of the puparia. This results in about 27 adult flies for each 100 larvae. If 10 or more adults were obtained some of them usually reproduced. The time required for 50% of the larvae to reach the third instar (ET_{50}) on the medium was 6.6 days (95% confidence limits: 5.9–7.3 days) and the first puparia were formed 6 or 7 days later. Thus the entire larval period occupied about 13–14 days. In Richardson's medium the first pupae developed from eggs in about 7 days. The high temperature (about 40° C.) in Richardson's medium caused by fermentation would account for some of this difference in development time, but some of the difference was probably caused by inadequacy of the chemical medium.

The effects of withdrawing vitamins are shown in Table II. Of the 10 vitamins in the complete medium only 7 (thiamine, riboflavin, pantothenic acid, nicotinic acid, choline, pyridoxine, and

biotin) are required by the larvae. Omission of *p*-aminobenzoic acid, inositol, or folic acid did not affect development and did not significantly alter the rate of growth of the larvae as indicated by the ET_{50}. The lethal effect of the lack of riboflavin, pantothenic acid, nicotinic acid, or biotin became apparent in the first instar. In these experiments the lethal effect of lack of thiamine began to appear in the second instar but was not statistically significant until the total larval mortality was considered. Finally, lack of choline and pyridoxine only became statistically significant when the mature larvae failed to pupate.

The puparium of the house fly is normally about 6.3 mm. long, according to West (1951). Those obtained on our control diet were 5.5±0.4 mm. long (mean and standard error) and 2.4±0.6 mm. wide, and they weighed 12.8±0.8 mg. The weights of those obtained from diets lacking *p*-aminobenzoic acid, inositol, and folic acid were 13.6±0.6 mg., 12.5±4.4 mg., and 12.5±0.9 mg., respectively.

The vitamin requirements of the house fly are apparently similar to the known requirements of most insects. Albritton's (1953) tables show that thiamine, riboflavin, nicotinic acid, pyridoxine, biotin, choline, and panthothenic acid are required by most insects that do not harbor symbiotes but that inositol and *p*-aminobenzoic acid are not. In common with our findings, no folic acid requirement is indicated for any species of Diptera in those tables. However, later work has shown that the growth rate of larvae of *Phormia regina* (Meig.) (Brust and Fraenkel 1955) and *Calliphora erythrocephala* (Meig.) (Sedee 1956) is increased by folic acid, and others using the folic acid antagonist 4-aminopteroylglutamic acid have indicated some requirement for this vitamin in the diets of *Drosophila melanogaster* (Meig.) (Goldsmith and Harnly 1950) and *M. domestica* (Mitlin, Konecky, and Piquett 1954).

Brookes (1957) reared the house fly aseptically on a medium consisting of casein, ribonucleic acid, adenine, guanine, uracil, McCollum-Davis salt mixture No. 185, a mixture of nine B vitamins, lecithin, cholesterol, water, and agar. On this diet the larvae grew about 10% slower than on a natural diet and weighed 30% to 40% less. He found that the larvae required biotin, folic acid, nicotinic acid, pantothenic acid, pyridoxine, riboflavin, and thiamine for growth. Choline, inositol, B_{12}, lipoic acid, and carnitine had no apparent effect. His results with folic acid and choline differ from ours. According to him, folic acid is required not only for growth but also for completion of metamorphosis, but its action is "spared" by ribonucleic acid.

These apparent contradictions may be resolved if there is a sufficient quantity of this vitamin in the house fly egg to provide for the first generation. It is obvious that caution must be exercised in judging the adequacy of a diet or the need for a dietary component unless at least one life cycle is involved, as the effects of omission of the various vitamins occur at different periods in the life history of the insect (see also the effect of ribonucleic acid on *P. affinis*; House and Barlow 1957a). The lethal effects may be due to gradual exhaustion of a supply of vitamin carried over from the previous generation, but the possibility that they result from a requirement for the vitamin for some specific developmental process is worthy of further investigation. Moreover, it is hoped that the medium can be improved until successive generations can be reared on it so that

TABLE II

EFFECT OF OMITTING VITAMINS, ONE AT A TIME, FROM A CHEMICALLY DEFINED DIET ON THE DEVELOPMENT OF ASEPTICALLY REARED HOUSE FLIES

VITAMIN OMITTED	LARVAE DYING, %			MATURE LARVAE PUPATING, %	ADULTS FROM PUPAE, %	REPRODUCTION[c]
	1st INSTAR	2nd INSTAR	TOTAL			
None	10.2	9.1	35.8	88.4	47.8	+ + +
Thiamine	19.0	40.3	98.1[b]	—	—	—
Riboflavin	96.1[b]	—	—	—	—	—
Pantothenate	30.8[b]	—	—	—	—	—
Nicotinic acid	45.2[b]	—	—	—	—	—
Choline Cl	18.6	11.8	50.9	1.2[b]	—	—
PABA[d]	16.0	11.5	34.5	98.4	31.0	+ +
Inositol	14.8	10.3	34.6	90.1	52.3	+ +
Pyridoxine	19.8	14.8	63.8	34.4[b]	—	—
Folic acid	3.9	5.5	24.1	96.3	36.9	+ +
Biotin	53.1[b]	—	—	—	—	—

[a]Statistically poorer than complete diet at 5% level of significance.
[b]Statistically poorer than complete diet at 1% level of significance.
[c]Each + represents reproduction on one of four replicates.
[d]*p*-aminobenzoic acid.

the cumulative effects of vitamin deficiencies can be studied over several generations.

REFERENCES CITED

Albritton, E. C. 1954. Standard values in nutrition and metabolism 380 pages. Philadelphia: W. B. Saunders Co.

Brookes, V. J. 1957. Personal communication.

Brust, M., and **G. Fraenkel.** 1955. The nutritional requirements of the larvae of a blowfly, *Phormia regina* (Meig.). Physiol. Zool. 28: 186–204.

Goldsmith, E. D., and **M. H. Harnly.** 1950. Reversal of action of folic acid antagonist 4-aminopteroylglutamic acid in *Drosophila melanogaster*. Cancer Research 10: 220.

Goulden, C. H. 1939. Methods of statistical analysis. 277 pages. New York: John Wiley & Sons, Inc.

House, H. L. 1954a. Nutritional studies with *Pseudosarcophaga affinis* (Fall.), a dipterous parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.). I. A chemically defined medium and aseptic culture technique. Canadian Jour. Zool. 32: 331–41.

1954b. Nutritional studies with *Pseudosarcophaga affinis* (Fall.), a dipterous parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.). II. Effects of eleven vitamins on growth. Canadian Jour. Zool. 32: 342–50.

1954c. Nutritional studies with *Pseudosarcophaga affinis* (Fall.), a dipterous parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.). III. Effects of nineteen amino acids on growth. Canadian Jour. Zool. 32: 351–57.

1954d. Nutritional studies with *Pseudosarcophaga affinis* (Fall.), a dipterous parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.). IV. Effects of ribonucleic acid, glutathione, dextrose, a salt mixture, cholesterol, and fats. Canadian Jour. Zool. 32: 358–65.

House, H. L., and **J. S. Barlow.** 1956. Nutritional studies with *Pseudosarcophaga affinis* (Fall.), a dipterous parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.). V. Effects of various concentrations of the amino acid mixture, dextrose, potassium ion, the salt mixture, and lard on growth and development; and a substitute for lard. Canadian Jour. Zool. 34: 182–89.

1957a. Effects of nuclein acids on larval growth, pupation, and adult emergence of *Pseudosarcophaga affinis* (Fall.). Nature 180: 44.

1957b. New equipment for rearing small numbers of *Pseudosarcophaga affinis* (Fall.) (Diptera: Sarcophagidae) for experimental purposes. Canadian Ent. 89: 145–50.

Mitlin, N., M. S. Konecky, and **P. G. Piquett.** 1954. The effect of a folic acid antagonist on the house fly. Jour. Econ. Ent. 47: 932–33.

Richardson, H. H. 1932. An efficient medium for rearing house flies throughout the year. Science 76: 350.

Sedee, J. W. 1956. Dietetic requirements and intermediary protein metabolism of the larvae of *Calliphora erythrocephala* (Meig.). 130 pages. Assen: Van Gorcum & Co., Ltd.

West, L. S. 1951. The housefly. 584 pages. Ithaca, N. Y.: Comstock Publishing Company, Inc. (p. 112.)

NOTES ON THE RICHARDIIDAE, WITH A REVIEW OF THE SPECIES KNOWN TO OCCUR IN THE UNITED STATES (DIPTERA, ACALYPTRATAE)[1]

GEORGE C. STEYSKAL

Grosse Ile, Michigan

ABSTRACT

Out of approximately 160 species, of 31 genera, in this essentially Neotropical family only five, representing four genera, are known from the United States. Keys to these are given, as well as to the five (Neotropical) species of *Epiplatea*. *E. hondurana* (= *E. erosa* Hendel, nec Loew) is described from British Honduras, *E. isthmi* from Panama, and *Odontomera limbata* from Florida and South Carolina. New synonymy: *Automola atomaria* (Wd.) (= *A. leopardina* Blanch.), *A. rufa* Cresson (= *Epiplatea dohaniani* Johnson), and *Odontomera ferruginea* Macq. (*O. dorotheae* Brimley). Distributional records are given for all species discussed. Descriptions and figures of the male postabdomen of *Richardia podagrica* F. and *O. nitens* Schiner are followed by a general discussion of the male postabdomen, leading to the conclusion that the group should be given family rank.

In common with all other families of the Acalyptratae, the almost wholly Neotropical family Richardiidae[2] remains poorly known. In Hendel's two great works on the group (1911; 1911a) 88 species were treated; Hennig (1937; 1938) raised the total to 127; and in 1950 Aczél catalogued 161 species, including three subspecies, distributed among 31 genera.

I here present a synopsis of the species known from the United States, which country includes the northern limits of the distribution of the group (with one new species, *Odontomera limbata*); synonymy in the genera *Automola* and *Epiplatea*; two new species of *Epiplatea*; and notes and figures of the male postabdomen of several forms.

KEY TO GENERA OF RICHARDIIDAE OF THE UNITED STATES

1 (2). Head twice as long as high; eyes horizontally oval; hind femora below with spines weak or lacking ..... **Coniceps** Loew

[1]Accepted for publication January 14, 1958.

[2]Reasons for considering the Richardiidae to be of family rank are given below in the discussion of the male postabdomen.

2 (1). Head not longer than high; eyes higher than long.
3 (4). Hind femora without spines below; propleural bristle strong; wing vein R_1 with a few setulae above ..... **Automola** Loew.
4 (3). Hind femora with spines below; propleural bristle weak or lacking.
5 (6). Occiput concave above the neck (Fig. 4) ..... **Odontomera** Macquart.
6 (5). Occiput convex above the neck (Fig. 23) ..... **Sepsisoma** Johnson.

Genus **Automola** Loew

This genus remains essentially as Hendel left it in 1911, with three species distinguished as follows, only one of which occurs in the United States.

1 (2). Abdomen with small black spots in a pale golden-felty network; legs pitchy brown (widespread in South America; Costa Rica; Mexico) ..... **A. atomaria** Wied.
2 (1). Abdomen otherwise; legs reddish, tarsi yellow.
3 (4). Abdominal tergites 3–5 each with two unhaired, whitish impressions at anterior margin; black apical spot on wing not broken into smaller crossmarks (South America) ..... **A. caloptera** Bigot.
4 (3). Abdomen without such impressions; apical wing spot broken into three crossbands, of which the basal one is isolated as a narrow stripe across *tp* from fore to hind margin of wing; tip of wing milky white (Southwestern United States; Mexico) ..... **A. rufa** Cresson.

Automola atomaria (Wiedemann)

Automola leopardina Blanchard, 1938, Rev. Argentina Ent. 1(3): 92, female, Puerto Bemberg, Misiones, Argentina. *New Synonymy.*

The above may be added to the synonymy cited in the Aczél catalogue (1950: 8). Blanchard states that his form is similar to *A. atomaria*, differing in possessing silvery-white pruinosity on the abdomen instead of pale yellow and in having short stumps of veins on R_2 (2) and M_2 (1) in the median transverse dark band. A female in the United States National Museum from Iquitos, Peru, which seems to me to be *A. atomaria*, has a stump on vein R_2 in the region of the dark band. The Museum also has examples from Atenas, Costa Rica. The species is thus known from Argentina, Paraguay, Bolivia, Peru, Brasil, British Guiana, Costa Rica, and Mexico.

Automola caloptera (Bigot)

The United States National Museum has specimens from Brasil (Boa Vista; Pará; Tapajos). The species is known from Bolivia, Peru, Brasil, and "Guiana."

Automola rufa Cresson

Automola rufa Cresson, 1906, Trans. Amer. Ent. Soc. 32: 282; Hendel, 1911, Deutsch. ent. Zts. 1911: 189; Gen. Ins. 113: 11.
Epiplatea dohaniani Johnson, 1921, Psyche 28: 58. *New Synonymy.*
Epiplatea dohaniniani (Jns.) Hennig, 1938, Rev. Ent. 7: 22; Aczél, 1950, Acta Zool. Lilloana 9: 10. *New Synonymy.*

The synonymy is rather obvious from Johnson's description. I have seen Cresson's type from Alamogordo, New Mexico, and specimens in the United States National Museum from Texas (Brewster County, Chisos Mts.; Corpus Christi; Donna; Luzello; Mercedes; San Antonio) and Mexico (Cuernavaca, bred from rotten cactus, *Opuntia* sp.; Querétaro, det. Aldrich as *E. dohaniani*). Marshall R. Wheeler has specimens from Mexico (Aguas Calientes) and Arizona (Cleator).

Genus **Coniceps** Loew

Coniceps niger Loew

Coniceps niger Loew, 1873, Smithsonian Misc. Coll. 256 (Monogr. Dipt. N. Am. 3): 178; Osten-Sacken, 1878, Smithsonian Misc. Coll. 270 (Cat. N. Am. Dipt., ed. 2): 187; Hendel, 1911, Deutsch. ent. Zts. 1911: 184; Gen. Ins. 113: 8; Curran, 1934, Fam. Gen. N. Am. Dipt.: 278.

This is the only known species in the genus. Hendel keys the genus in a group lacking femoral spines. The larger specimens which I have examined, however, have a few distinct spines on the hind femora. The species is cited from "Texas" by Loew, and no other specimens seem to be mentioned in the literature. I have seen material from Texas (Alvin; Dallas; Waco) and Kansas (Baldwin; Fort Scott; Lawrence; Manhattan; Mildred).

Genus **Odontomera** Macquart

This is one of the larger genera in the Aczél catalogue, including 18 nominate forms. Two species have been found in the United States, distinguishable as follows. Both are forms which are nearly wholly yellow.

1 (2). Wings (Fig. 3) with distinct brown costal margin from root to tip of 4th vein; scutellum blackish apically between the bristles ..... **O. limbata** n. sp.
2 (1). Wings lacking brown costal margin; scutellum with lateral black marks or wholly yellow ..... **O. ferruginea** Macquart.

Odontomera ferruginea Macquart

(Figs. 1, 2)

Cyrtometopa ferruginea (Macquart) Aldrich, 1905, Smithsonian Misc. Coll. 46 (Cat. N. Am. Dipt.): 599; Johnson, 1913, Bull. Am. Mus. Nat. Hist. 32: 83.
Odontomerus dorotheae Brimley, 1925, Ent. News 36: 74 (referred to Trypetidae, but in author's separates referred to Ortalidae and generic reference corrected to *Odontomera*). *New Synonymy.*
Odontomera dorotheae Brimley, 1938, Ins. N. Carolina: 383. *New Synonymy.*
Odontomera ferruginea (Macq.) Frost, 1929, Ent. News 40: 87.

I have examined the types of *Odontomerus dorotheae* and find them conspecific with material which I determine on the basis of Hendel's descriptive notes as *Odontomera ferruginea*. I would therefore add the above citations to those given by Aczél (1950: 34).

The eyes of *O. ferruginea* in fresh material are brassy green, with two narrow, oblique, reddish-purple stripes (Fig. 1).

The male terminalia are as in figure 2; the epandrium is wholly yellow, somewhat extended ventrally and there furnished with tufts of setae; the surstyli and postgonites are broader than in *O. limbata;* the aedeagus is much as in *O. nitens*, not bulbous apically.

The distribution of the species is given by Aczél as southward to Paraguay and Bolivia, but how many of the records actually refer to Macquart's species is rather doubtful. Macquart did not cite a locality. Aldrich cited localities in Mexico (Orizaba; Morelos; Vera Cruz); Johnson recorded it from Florida (Crescent City); and Frost cited Pennsylvania, referring to "published" records of Cresson, which however do not seem to exist.

I have seen specimens from New Jersey (Moorestown), Maryland (Chesapeake Beach; College Park, Glen Echo; Prince Georges County; Shadyside; Tacoma Park), District of Columbia, Virginia (Alexandria; Bon Air; Falls Church; Glencarlyn), North Carolina (Edgecombe County; Raleigh), South Carolina (McClellanville), Georgia ("Southern Georgia"), and Florida (Gifford). The Florida material lacks the lateral scutellar spots and the wing markings are very pale, but otherwise seems identical with the others.

Odontomera limbata Steyskal, new species

(Figs. 3–5)

Male. Length of wing, 4.6–5.2 mm.

Body and appendages nearly wholly yellow; spot at apex of scutellum between the bristles and dorsal arch of epandrium black; tibiae and tarsi, especially of hind legs, somewhat brownish; all bristles and setae black.

Wing (Fig. 3) hyaline, with yellow to brownish veins, brown costal seam and brown seam along *tp*.

Head as in figure 4. Color of eye in life not known.

Femora with ventral spines as follows: fore femora 3–5, middle femora 8–12, hind femora 9–13.

Terminalia as in figure 5; epandrium not extended ventrally nor with tufts of setae; surstyli and postgonites very slender, the latter with acute, curved, black apical tooth; aedeagus bulbous at tip, with membranous distal extensions and tuft of hairs on one side.

Female. Length of wing, 5.0 mm. Abdomen wholly yellow. Otherwise similar to male.

Holotype and one paratype (males), Palm Beach County, Florida, March 28, 1946 (O. D. Link), collected in McPhail trap, S.P.B. Acc. No. 59032, in United States National Museum; one male paratype, McClellanville, South Carolina, May 16, 1944 (H. and M. Townes), in my collection; *allotype* (female), La Belle, Florida, July 16, 1939 (P. B. Lawson), in University of Kansas.

Odontomera limbata differs from *O. ferruginea* as in the preceding key, in lacking a subbasal wing band, and in details of the postabdomen. It is apparently related to *O. marginalis* Walker, from the Amazon region, and to *O. costalis* Hendel, from Argentina, the only other species with brown costal wing margin. *Odontomera marginalis* is poorly described and may be a *Setellia;* it is stated to have black antennae and black knobs on the halteres. *Odontomera costalis* has pitchy black sternum and abdomen, also pitchy brown legs, and the costal seam of wing basally broad; the scutellum is "yellowish-red."

Genus **Sepsisoma** Johnson

Sepsisoma flavescens Johnson

(Figs. 22, 23)

Sepsisoma flavescens Johnson, 1900, Ent. News 11: 327; Smith, 1910, Ann. Rept. New Jersey State Mus. for 1909: 800; Hendel, 1911, Deutsch. ent. Zts. 1911: 379; Gen. Ins. 113: 37; Frost, 1929, Ent. News 40: 87; Brimley, 1938, Ins. N. Carolina: 383; Aczél, 1950, Acta Zool. Lilloana 9: 37.

This, the single species of *Sepsisoma* in the United States, may be distinguished from the other 10 known species by its nearly wholly yellowish color, only the tibiae being blackish.

The eyes of fresh specimens (Fig. 23) are brassy green above and in two broad, obliquely horizontal bands, the remainder is reddish purple.

The male postabdomen (Fig. 22) has the external end of the aedeagal apodeme (phallobase) with a stout, recurved hook; the aedeagus long and slender, with rather simple tip; the surstyli stout, incurved, with external humps before the acute tips; the postgonites also stout and with anterior fringe of setae; the ejaculatory apodeme with almost circular blade.

Johnson described the species from Westville, New Jersey, and Smith cited that locality and Trenton and Wenonah, New Jersey. Hendel cited a specimen from Washington, D. C. Brimley recorded material from Raleigh, Fayetteville, and Springhope, North Carolina. Frost's reference

EXPLANATION OF FIGURES

FIGS. 1, 2.—*Odontomera ferruginea* (Macq.): eye pattern (1) and posterior view of male terminalia (2).

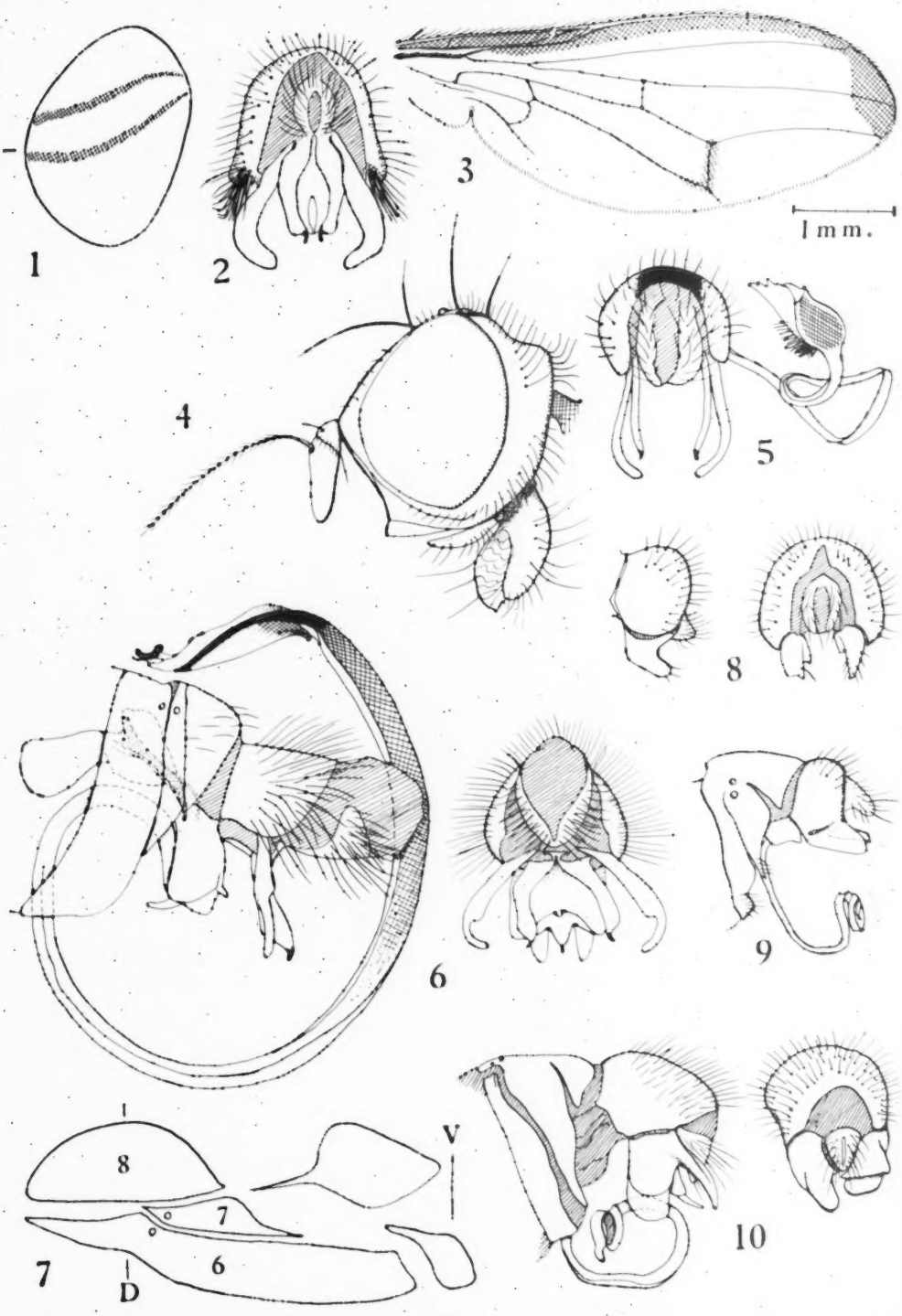
FIGS. 3–5.—*Odontomera limbata*, n. sp.: wing (3), head (4), and posterior view of male terminalia (5).

FIGS. 6, 7.—*Odontomera nitens* Schiner: left side and posterior views of male postabdomen (6), diagram of protandrium drawn as if split along mid-ventral line and laid flat. D—mid-dorsal line; V—mid-ventral line; 6, 7, 8—abdominal segments.

FIG. 8.—*Epiplatea isthmi*, n. sp.: lateral and posterior views of male terminalia (epandrium, surstyli, and proctiger).

FIG. 9.—*Epiplatea erosa* Loew: left lateral view of male postabdomen.

FIG. 10.—*Epiplatea hondurana*, n. sp.: left lateral and posterior views of male postabdomen.


1
2
3
1 mm.
4
5
8
6
9
V
8
7
7
6
D
10

is to published records from Pennsylvania by Cresson, which however do not seem to exist.

I have seen material from New York (Long Id.), New Jersey (Riverton), Maryland (Bethesda; Glen Echo; Prince Georges County), District of Columbia, Virginia (Alexandria, Mt. Vernon), North Carolina (Fayetteville; Raleigh), North Carolina-Tennessee (Great Smoky Mts. Nat. Park), Ohio (Ironton; Vinton), Indiana (Crawfordsville), Iowa (Ames), and Kansas (Lawrence).

Genus **Epiplatea** Loew

With the removal of *Epiplatea dohaniani* (*v. Automola rufa, supra*) and *E. scutellaris* Coq., which examination of type shows to be an Otitine and which will be reported upon elsewhere, an homogeneous group remains, no species of which is known from the United States.

KEY TO KNOWN SPECIES OF **EPIPLATEA**

1 (4). Median band of wing broad, becoming suddenly narrowed behind fourth vein; *ta* in small area of infuscation; apical mark on wing lacking or slight; fifth tergite of female abdomen without swellings.

2 (3). Prescutellar area occupied by a band of white pruinosity behind posterior dorsocentral bristles; apex of wing milky, without trace of brown mark; base of abdomen only slightly paler than remainder; *male*: hind tibiae straight (Fig. 12); terminalia as in figure 9, symmetrical (Cuba; Puerto Rico; San Domingo; generitype) ..... **E. erosa** Loew

3 (2). Prescutellar white-pruinose marks in form of two dots, one behind each posterior *dc*; tip of wing hyaline, with slight brown mark on extreme apex; base of abdomen broadly yellow; *male*: hind tibiae curved (Fig. 13); terminalia as in figure 10, strongly asymmetrical (Honduras) ..... **E. hondurana**, n. sp.

4 (1). Median band of wing narrow, of equal width from first vein to posterior margin; *ta* not infuscated; distinct apical wing mark present.

5 (6). Thoracic dorsum blackish, with gray pruinosity; apical wing mark ending at third vein; cell C brown with central one-third hyaline; medial wing band along proximal margin perpendicular all the way to costa; male hind tibiae ordinary (Paraguay) ..... **E. recta** Hendel

6 (5). Thorax yellowish to reddish; apical wing mark extending to fourth vein; cell C hyaline, with central brown mark.

7 (8). Medial wing band turning basad anterior to second vein; male hind tibiae ordinary (Peru; Brasil; British Guiana) ..... **E. arcuata** Hendel

8 (7). Medial wing band turning basad only very close to costa; prescutellar white-pruinose marks consisting of separated spots behind posterior *dc*; *male*: hind tibiae swollen apically, projecting beyond base of tarsus (Fig. 11); terminalia as in figure 8, subsymmetrical (Panamá) **E. isthmi**, n. sp.

Epiplatea arcuata Hendel

Epiplatea arcuata Hendel, 1911, Deutsch. ent. Zts. 1911: 192; Gen. Ins. 113: 13, pl. 1, ff. 15–17; Curran, 1934, Bull. Am. Mus. Nat. Hist. 66: 423; Fam. Gen. N. Am. Dipt.: 276; Hendel, 1936, Ann. Naturh. Mus. Wien 47: 81; Hennig, 1937, Rev. Ent. 7: 22; Aczél, 1950, Acta Zool. Lilloana 9: 9.

I have not seen this species. Hendel makes no mention of the peculiar modification of the hind tibiae in the male which is so striking in *E. isthmi*, n. sp. (v.i.). He also states "wie bei *E. erosa* . . . vor dem Schildchen . . . silberweiss bereift." Inasmuch as the form which Hendel identified with *E. erosa*, and which I am describing below as *E. hondurana*, n. sp., differs from the insular form which I am indentifying as *E. erosa* in having the prescutellar pruinosity broken into two spots, this character in *E. arcuata* must remain in some doubt.

The species was described from Meshagua, Peru; Curran recorded it from Kartabo and Kaieteur, British Guiana; and Hendel in 1936 reported it from Taperinha, Pará, Brasil.

Epiplatea erosa Loew

(Figs. 9, 12)

Epiplatea erosa Loew, 1867, Berlin. ent. Zts. 11: 325, pl. 2, f. 25; 1873, Smithsonian Misc. Coll. 256 (Monogr. Dipt. N. Am. 3): 194, pl. 9, f. 24; Osten-Sacken, 1878, Smithsonian Misc. Coll. 270 (Cat. N. Am. Dipt., ed. 2): 187; Wolcott, 1936, Jour. Agric. Univ. Porto Rico 20: 373.

Loew described and figured this species from Cuba. Wolcott recorded it from Puerto Rico. I have examined specimens in the United States National Museum from San Domingo (San Francisco Mts., August 28, 1905, August Busck) which agree well with Loew's description, including the reference to "an almost silvery-white transverse crossband" on the thoracic dorsum, and have prepared figures of the male hind tibia (Fig. 12) and terminalia (Fig. 9) from them.

I have also examined the material from British Honduras, on the basis of which Hendel figured *E. erosa*, and find it to represent another species, one which I am describing below as *E. hondurana*, n. sp.

Epiplatea hondurana Steyskal, new species

(Figs. 10, 13, 15–18)

Epiplatea erosa Hendel, 1911, Deutsch. ent. Zts. 1911: 192; Gen. Ins. 113: 13, pl. 1, f. 18. *Not* Loew, 1867.

Length of wing, 3.3 to 3.6 mm.

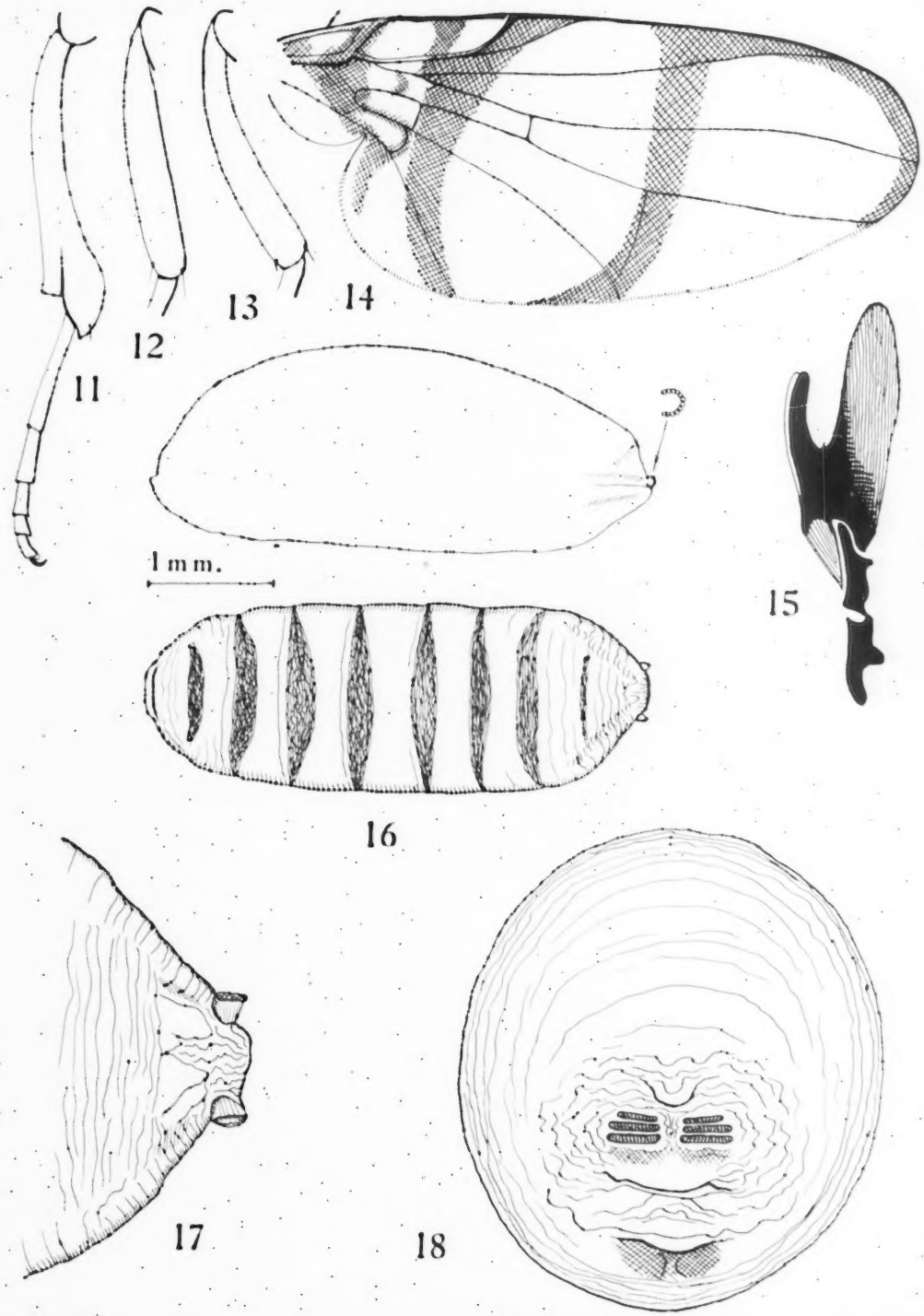
Male. Thoracic dorsum light brown, with three slightly darker longitudinal lines, a pair of silvery white roundish spots posterad of the dorsocentral bristles, and silvery white notopleural areas. Wings as figured by Hendel; the preapical dark crossband at third vein extending from level

EXPLANATION OF FIGURES

FIGS. 11–13.—Hind tibiae of males of *Epiplatea isthmi*, n. sp. (11, with tarsus), *Epiplatea erosa* Loew (12), and *Epiplatea hondurana*, n. sp. (13).

FIG. 14.—*Epiplatea isthmi*, n. sp.: wing.

FIGS. 15–18.—*Epiplatea hondurana*, n. sp.: cephalopharyngeal skeleton (15), profile (with inset of anterior spiracle) and ventral view of puparium (16), dorsal view of anterior end of puparium (17), and posterior end of puparium (18).


11
12
13
14
1 mm.
15
16
17
18

of posterior crossvein two-thirds distance to end of vein; apex of wing beyond crossband hyaline, with slight darkening at extreme apex.

Hind tibiae (Fig. 13) slightly arcuate, but of ordinary form.

Abdomen black, broadly yellow at base; fifth tergite as long as fourth; postabdomen (Fig. 10) with surstyli strongly asymmetrical and aedeagus long and coiled, simple at tip and without special armature.

Female. Similar to male; abdomen covered with rather long, erect hair; fifth tergite simple, less than one-third as long as fourth tergite.

Puparium. Length, 3.9 to 4.1 mm. Shape as in figure 16; color rather light yellow-brown, shining except on vestiges of locomotor fasciae, which are minutely transversely rugulose, without spinules, and extend from venter halfway up sides. Anterior spiracles directed laterad, each with 10 to 12 papillae arranged in three-fourths of a circle (Figs. 16, 17). Posterior end of puparium (Fig. 18) with spiracles consisting of two groups of three slits in almost parallel arrangement, without distinct peritreme surrounding each group nor with any distinct buttons of scars, but surrounded by areas of irregular wrinkling. Anal orifice not clearly discernible. Cephalopharyngeal skeleton (Fig. 15), retrieved from puparium and relaxed and cleaned in boiling NaOH solution, 1 mm. long, with short and narrow dorsal cornua, broad but thin and pale ventral cornua, and hypostomal sclerite in two lateral parts connected by a narrow posteroventral strip; mouth hooks with two blunt teeth.

Holotype (male), allotype, and nine paratypes (three males, 6 females), each with puparium, Manatee, British Honduras, January, 1902, on diseased cocoanut palm (J. T. Seay), in United States National Museum, except one pair of paratypes retained in my collection.

As noted in the key to species, this form is very closely related to *E. erosa* Lw.

Epiplatea isthmi Steyskal, new species

(Figs. 8, 11, 14)

Length of wing, 3.5 to 3.9 mm.

Male. Thoracic dorsum concolorous yellow-brown, with a pair of roundish silvery white spots posterad of dorsocentral bristles and silvery white notopleural areas.

Wings as in figure 14; the costal cell hyaline, with isolated brown spot apicad of middle; *ta* not in brown spot; median brown crossband parallel-sided, turning basad near posterior margin of wing and very close to costa; costal margin with distinct brown seam from median band to apex of fourth vein.

Hind tibiae as in figure 11, slightly arcuate, with marked apical swelling, from middle of which the tarsi extend, the tip of the swelling pointed.

Abdomen brown to piceous, not paler basally, the apical tergite of preabdomen equal in length to the one preceding it; last segment of postabdomen (epandrium) as in figure 8, the surstyli nearly symmetrical.

Female. Similar to male; hind tibiae simple, slightly arcuate; abdomen with short, erect hair, the fifth tergite half as long as the fourth, tumid apicolaterally, leaving a triangular mediobasal area appearing sunken.

Holotype (male), Close's, Cano Saddle, Canal Zone, Panamá, May 2, 1923 (R. C. Shannon); allotype, female, La Campana, Panamá, Jan.-Mar., 1938 (Jas. Zetek); paratypes: male, Coco Solo, C. Z.; females, 1, Barro Colorado, C. Z., Nov., 1937, fruit fly trap (Jas. Zetek); 1, La Campana, Panamá, Sept., 1937, fruit fly trap (Jas. Zetek); 2, same data as allotype; in United States National Museum, except male paratype and one female paratype from La Campana retained in my collection.

As shown in the key to species, *E. isthmi* is related to *E. arcuata*, differing therefrom in wing markings, tumid apicolateral corners of fifth tergite of female, details of male terminalia, apically swollen hind tibiae of male, etc. In no other species has this peculiar development of the male hind tibia been noted.

Epiplatea recta Hendel

Epiplatea recta Hendel, 1911, Deutsch. ent. Zts. 1911: 193; Gen. Ins. 113: 13, pl. 1, f. 19; 1933, Rev. Ent. 3: 222; Aczél, 1950, Acta Zool. Lilloana 9: 10.

This species is known only from Paraguay; I have not seen it.

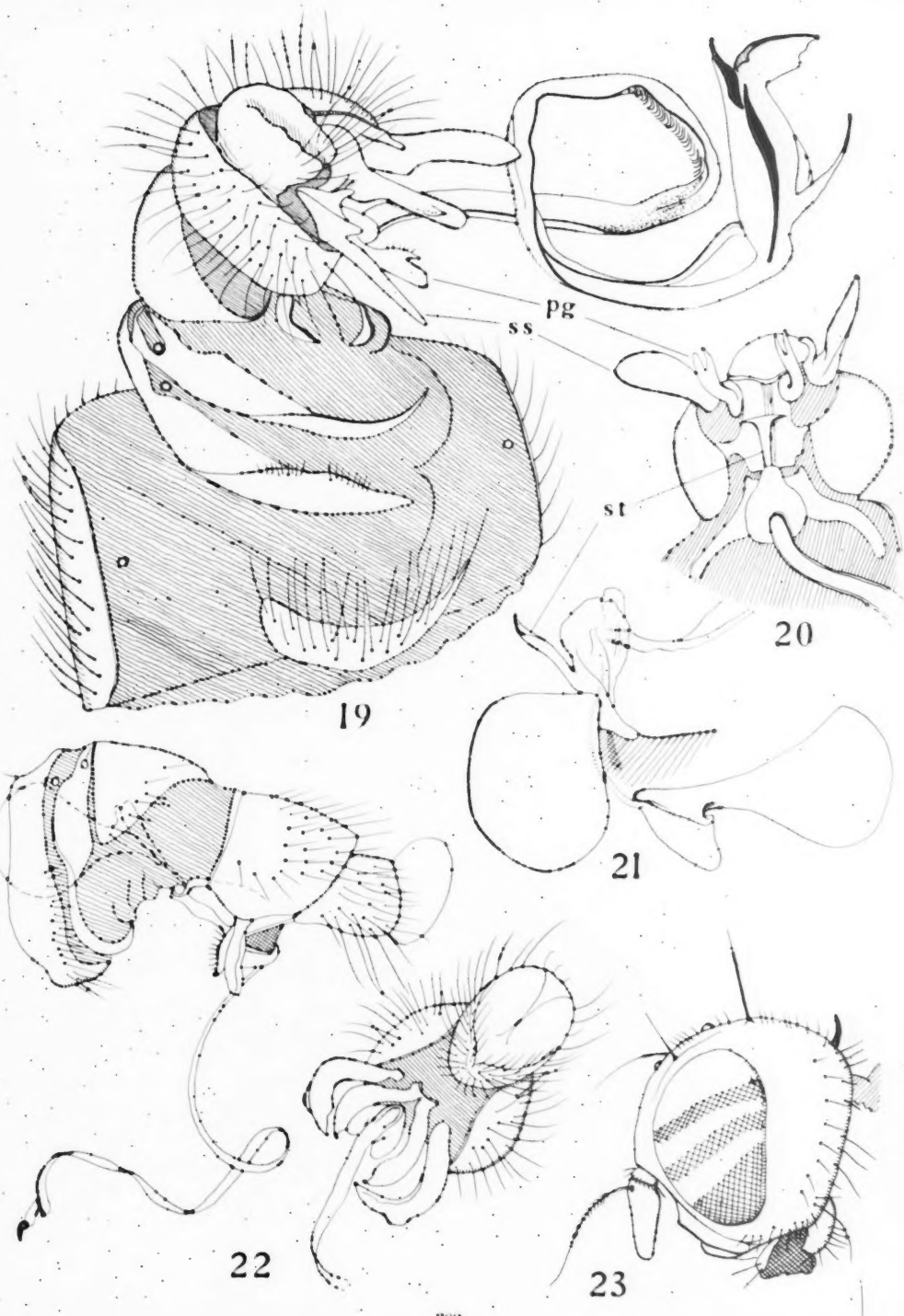
THE MALE POSTABDOMEN

Besides the examination of the postabdomen of the species of *Odontomera*, *Sepsisoma*, and *Epiplatea* for purposes of specific differentiation, two species were also examined with a view to establishing the character of the postabdomen in the family, since very little data until now have been available. Cole (1927: 444, 495, Fig. 251) gave a figure of *Richardia podagrica* in which little detail is discernible. Souza Lopes (1936: 477) presented partial, species-differentiation figures of one species each of the genera *Setellia*, *Hemixantha*, and *Ozaenina*. In the present discussion I am continuing use of the terminology adopted in my recent review of the acalyptrate postabdomen (Steyskal 1957).

EXPLANATION OF FIGURES

FIGS. 19–21.—*Richardia podagrica* Fabr.: lateroventral view of fifth abdominal segment and postabdomen (19), lateroventral view of andrium, bristles omitted (20), and left lateral view of epandrium with phallobase and ejaculatory apodeme (21). pg—postgonite; ss—surstylus; st—spinus titillatorius.

FIGS. 22, 23.—*Sepsisoma flavescens* Jns.: left lateral and posterior views of postabdomen (22) and head (23).


pg
ss
st
19
20
21
22
23

Richardia podagrica F.

(Figs. 19–21)

Protandrium.—Tergites on left side only, those of segments 6 and 7 apparently fused with their sternites and with a single spiracle each; some sclerotization, apparently secondary, in anterior part of genital pouch.

Andrium.—Strongly lateriverted as result of strophic displacement, but practically symmetrical; epandrium rather simple, bearing a well developed pair of surstyli, each of which is somewhat spatulate in form and with a posterobasal process; hypandrium apparently consisting of two portions, an anterior portion (? sternite 9) bearing the aedeagus, and a posterior portion (? sternite 10) bearing a large pair of apically bifid postgonites. The aedeagus is long and coiled, with some short pile in mid-portion and rather complex apically. A T-shaped spinus titillatorius (Figs. 20, 21, st) is developed and a rather short and simple aedeagal apodeme. The ejaculatory apodeme (Fig. 21) is large and widely expanded at the end opposite the vesiculum.

Proctiger.—A pair of soft lobes bearing long hairs.

Source of material.—Pucallpa, Peru.

Odontomera nitens Schiner

(Figs. 6, 7)

Protandrium.—Largely on left side, with some areas of apparently secondary sclerotization in genital pouch; tergite 8 roughly symmetrical; spiracles 6 and 7, one each within sclerotic areas just left of meson (see diagram, Fig. 7).

Andrium.—Symmetrical; epandrium rather simple, bearing a well developed pair of surstyli, each of which is curved mesad and suddenly constricted beyond middle; hypandrium in two parts, the anterior part somewhat columnar and massive, with aedeagus reflexed from its apex, the posterior part narrowly connected with the anterior part and consisting largely of a pair of strong postgonites. The aedeagus is long and loosely coiled, smooth and with some specialized structures apically. The aedeagal apodeme is small, short and straight, hardly extending toward interior from base of hypandrium. The ejaculatory apodeme is rather small for a fly with so long an aedeagus; vas deferens also short.

Proctiger with ventral sclerite bearing long hairs and with soft membranous termination.

Source of material.—Jalastoc, Morelos, Mexico.

RÉSUMÉ

The system of levers developed in the hypandrium of the Trypetidae, Platystomidae, and Pyrgotidae, in which the main or anterior body of the hypandrium is in the shape of a horseshoe and the aedeagal apodeme is more or less curved forward and connected with the "horseshoe" (Vordere Gabelplatte of Hennig) by a pair of lateral processes is lacking in all of the Richardiidae examined. Instead a more or less massive "phallobase" is present, with short and more or less straight aedeagal apodeme and anteriorly free-ending lateral arms.

The characteristic development of the posterior part of the hypandrium into a part of strong claspers, or postgonites, apparently cooperating with the surstyli, is present in all forms (including species of *Richardia, Odontomera, Sepsisoma, Setellia, Hemisantha, Ozaenina*) except *Epiplatea*, which is aberrant in several respects.

The aedeagus, as in other Otitiformes, is long and slender, but lacks the special armature along its length that is found in the Otitidae (incl. Pterocallidae) and also lacks the special end structures found in the Platystomidae, although at least in *Richardia podagrica* and *Odontomera limbata* specialization of the end of the aedeagus of a different type occurs.

The epandrium and surstyli are also characteristic and differ greatly from the Ulidiinae, which otherwise most resemble the Richardiidae.

On the above considerations and those of the wing venation and other characters commonly used, I would consider the Richardiidae to be of family rank. The only other alternative, I believe, would be to group all of the old Otitidae (including Platystomidae, Ulidiidae, Pterocallidae, etc.), as well as the Pyrgotidae and Trypetidae, into one family. This course would hardly be consonant with modern developments.

REFERENCES CITED

Aczél, M. L. 1950. Catálogo de la subfamilia americana "Richardiinae" (Dipt. Acalypt. "Otitidae"). Acta Zool. Lilloana 9: 1–47.

Cole, F. R. 1927. A study of the terminal abdominal structures of male Diptera (two-winged flies). Proc. California Acad. Sci. (4)16: 397–499.

Hendel, F. 1911. Die Arten der Dipteren-Subfamilie Richardiinae. Deutsch. ent. Zeitschr. 1911: 181–270, 367–96.

1911a. Diptera, Fam. Muscaridae, Subfam. Richardiinae. Genera Ins. fasc. 113: 1–56, Pls. 1–3.

Henning, W. 1937. Beiträge zur Systematik der Richardiiden (Dipt.). Rev. Ent. 7: 21–34, 306–16, 484–6, 8: 111–22.

1938. Neue Beiträge zur Systematik der Richardiiden und Tyliden. Arb. morphol. taxon. Ent. 5: 8–15.

Souza Lopes, H. de. 1936. Sôbre três espécies novas de Richardiidae do Brasil (Dipt.). Rev. Ent. 6: 475–80.

Steyskal, G. C. 1957. The postabdomen of male acalyptrate Diptera. Ann. Ent. Soc. America 50: 66–73.

ACTIVITY OF DEHYDROGENASE ENZYMES DURING THE METAMORPHOSIS OF THE MEALWORM, TENEBRIO MOLITOR LINNAEUS[1]

DANIEL LUDWIG AND MARY C. BARSA
Department of Biology, Fordham University

ABSTRACT

No evidence was found for formic, beta-hydroxybutyric, choline, or glutamic dehydrogenases in the larva; glutamic appeared towards the end of the pupal stage. Succinate and alpha-glycerophosphate did not require DPN for their oxidation, but its addition greatly stimulated utilization of the latter substrate. Alcohol, glucose, glutamic, and malic dehydrogenases could not act without DPN; isocitric dehydrogenase and malic enzyme required TPN. Lactic dehydrogenase did not require DPN in the larva; however, in the pupa and adult its addition increased the oxidation of lactate. Curves for the activities of malic and succinic dehydrogenases and the malic enzyme were U-shaped during metamorphosis. Since the activity of succinic dehydrogenase was lower than those of the other two enzymes, it could be a determining factor in the U-shaped respiratory curve. The high activity of malic enzyme coupled with a low value for lactic dehydrogenase makes the accumulation of lactate unlikely, since the malic enzyme would convert pyruvate to malate under anaerobic conditions.

The O_2 consumption of holometabolous insects follows a U-shaped curve during metamorphosis. Since this phenomenon was described by Krogh (1914) various explanations have been proposed. Krogh (1914) and Fink (1925) believed the changes in O_2 consumption to be associated with different degrees of tissue organization. Wolsky (1938), Williams (1950), and Ludwig (1953) found U-shaped activity curves for cytochrome oxidase during the pupal stages of the fruit fly *Drosophila melanogaster*, the moth *Platysamia cecropia*, and the Japanese beetle *Popillia japonica*, respectively. They correlated this activity with the rate of O_2 consumption. Wolsky (1941) with *D. melanogaster*, and Ludwig and Barsa (1955) with *P. japonica*, found a similar correlation between the activity of succinic dehydrogenase and respiratory metabolism. However, Ludwig and Barsa (1956) reported that the activity curves of cytochrome oxidase and of succinic dehydrogenase are not U-shaped during the metamorphosis of the mealworm, *Tenebrio molitor*. Hence, these two enzymes may not be controlling factors in the pupal respiration of this insect.

Agrell (1949) described total dehydrogenase activity and the specific activities of malic, citric, and glutamic dehydrogenases as U-shaped during the metamorphosis of the blowfly, *Calliphora erythrocephala*. Hence, a study of various dehydrogenases of the mealworm, *T. molitor*, was undertaken to find a possible correlation between their activities and the U-shaped respiratory curve.

MATERIAL AND METHODS

Larvae were obtained from a mixed culture maintained at room temperature. Prepupae were collected from this culture and placed at 30° C. They were examined daily and the newly molted pupae were placed in beakers and also kept at 30° C. Pupae of known ages, within 24 hours, were thus obtained.

The activities of succinic, malic, glucose, L-glutamic, alpha-glycerophosphate, lactic, formic, beta-hydroxybutyric, choline, and isocitric dehydrogenases and the malic enzyme were determined by the Thunberg method as given by Umbreit, Burris and Stauffer (1945, p. 126). Insects were homogenized by means of a motor-driven glass homogenizer for 1 minute in 0.03 M phosphate buffer, except for isocitric dehydrogenase, where veronal buffer was used since the phosphate ion interferes with the activity of this enzyme. In all cases, the buffers were adjusted to a pH of 7.4. A 3 percent homogenate (1 ml.) was incubated at 30° C. for 30 minutes, and when DPN or TPN was used, the homogenate was incubated with 0.5 ml. of 0.2 percent DPN or with 0.5 ml. of 0.1 percent TPN to oxidize the endogenous substrate. The smaller concentration of TPN was used because the addition of larger amounts did not increase enzyme activity. The homogenate was then placed in the side arm cap of the Thunberg tube. In the body of the tube were placed 1 ml. of 1/10,000 percent methylene blue, 1 ml. of substrate, and sufficient buffer to bring the final volume to 6 ml. In determining malic dehydrogenase activity, 0.5 ml. of 0.24 M KCN was added to prevent inhibition by the oxalacetate formed (Green, 1936). In measuring the activity of succinic dehydrogenase, 0.5 ml. of a mixture of 0.005 M $CaCl_2$ and 0.005 $AlCl_3$ was added. TPN was used in studies of isocitric dehydrogenase and the malic enzyme. In the former determinations, 0.5 ml. of 6×10^{-3} M $MnCl_2$, and in the latter, 0.5 ml. of 0.033 M $MgSO_4$ was added. In each case, the supplementary solutions were added before the final dilution of the homogenate. The tubes were evacuated for 5 minutes and were then inverted to add the homogenate contained in the side arm to the mixture in the main portion of

[1]This work was supported in part by the Medical Research and Development Board, Office of the Surgeon General, Department of the Army, under Contract No. DA-49-007-MD-441. Accepted for publication January 6, 1958.

the tube, thus bringing the final concentration of homogenate to 0.5 percent. The tubes were then placed in a constant temperature bath at 30° C., and the time required for 90 percent reduction of methylene blue was determined by visually matching the color with that of a standard tube. This standard contained all of the components of the other tubes except that the homogenate had been previously inactivated by boiling and the methylene blue was diluted to $\frac{1}{10}$ the usual concentration.

OBSERVATIONS

Table I lists the activities (1/time in minutes for 90 percent decoloration of methylene blue) for homogenates of mealworm larvae. Each value is an average of at least 10 determinations. Since the activities of enzymes of different insects are often very different, in most cases the homogenate was divided into 4 parts; the first was used without substrate, the second with substrate but no DPN, the third with DPN but no substrate, and the fourth with both substrate and DPN. When malate and isocitrate were used as substrates, the homogenate was divided into 6 parts. Four were used as indicated above, the fifth with TPN and no substrate, and the sixth with both substrate and TPN. In reading the table, the values in the first and second, third and fourth, and fifth and sixth columns should be compared. There was no evidence of dehydrogenase activity when sodium formate, beta-hydroxybutyric acid, L-glutamic acid, or choline chloride were used as substrates. Alcohol, malic and glucose dehydrogenases did not act without the addition of DPN, while succinic and lactic did not require it.

TABLE I

DEHYDROGENASE ACTIVITY OF 0.5 PERCENT HOMOGENATES OF MEALWORM LARVAE AT 30° C. ACTIVITY IS EXPRESSED AS 1/TIME FOR 90 PERCENT DECOLORATION OF METHYLENE BLUE

SUBSTRATE	HOMOGENATE, NO SUBSTRATE (CONTROL)	HOMOGENATE +SUBSTRATE, NO DPN	HOMOGENATE +DPN, NO SUBSTRATE (CONTROL)	HOMOGENATE +SUBSTRATE +DPN	HOMOGENATE +TPN, NO SUBSTRATE (CONTROL)	HOMOGENATE +TPN+ SUBSTRATE
Ethyl alcohol	0.012	0.012	0.017	0.056	———	———
Choline chloride	0.019	0.018	0.023	0.021	———	———
Sodium formate	0.026	0.026	0.037	0.037	———	———
d-glucose	0.011	0.012	0.017	0.028	———	———
L-glutamic acid	0.011	0.011	0.013	0.014	———	———
Sodium alpha-glycerophosphate	0.023	0.034	0.030	0.079	———	———
Beta-hydroxybutyric acid	0.020	0.021	0.029	0.032	———	———
Sodium isocitrate	0.012	0.014	0.018	0.018	0.021	0.286
Sodium lactate	0.013	0.021	0.022	0.030	———	———
Sodium malate	0.010	0.009	0.016	0.323	0.062[a]	0.189[a]
Sodium succinate	0.022	0.043	0.015	0.033	———	———

[a]Homogenate contained $MgSO_4$, no KCN.

TABLE II

DEHYDROGENASE ACTIVITY DURING THE METAMORPHOSIS OF THE MEALWORM AT 30° C. ACTIVITY IS EXPRESSED AS 1/TIME IN MINUTES FOR 90 PERCENT DECOLORATION OF METHYLENE BLUE

DEHYDROGENASE	LARVA	PREPUPA	PUPA						ADULT (NEWLY EMERGED)
			Newly MOLTED	1-day	2-day	3-day	4-day	5-day	
Alcohol	0.039	0.038	0.034	0.041	0.032	0.036	0.038	0.040	0.038
Glucose	0.011	0.006	0.007	0.006	0.007	0.008	0.007	0.009	0.008
Glutamic	———	———	———	———	———	———	———	0.005	0.010
Alpha-glycero-phosphate I	0.038	0.049	0.049	0.047	0.054	0.050	0.047	0.051	0.037
Alpha-glycero-phosphate II	0.011	0.006	0.005	0.005	0.005	0.006	0.005	0.005	0.009
Isocitric	0.265	0.224	0.185	0.171	0.171	0.171	0.183	0.171	0.141
Lactic I	———	0.003	0.004	0.002	0.001	0.003	0.003	0.003	0.010
Lactic II	0.008	0.002	0.003	0.003	0.003	0.003	0.002	0.005	0.004
Malic	0.307	0.165	0.130	0.105	0.115	0.139	0.175	0.200	0.280
Malic enzyme	0.127	0.075	0.056	0.053	0.068	0.069	0.053	0.066	0.099
Succinic	0.021	0.008	0.007	0.005	0.005	0.006	0.007	0.010	0.019

Alpha-glycerophosphate dehydrogenase acted without the addition of DPN, but its presence greatly increased activity. Isocitric dehydrogenase required TPN.

The activities of the dehydrogenase enzymes during the metamorphosis of the mealworm at 30° C. are given in Table II and figure 1. They were obtained by subtracting the rate of the control (homogenate without substrate) from that of the homogenate containing substrate. The activities of malic and succinic dehydrogenases and of malic enzyme follow U-shaped curves. The activity of alcohol dehydrogenase remained constant while that of glucose decreased during the change from larva to prepupa and then remained constant during the remainder of metamorphosis. Glutamic dehydrogenase, which was not present in the larva, appeared during the latter part of the pupal stage. Lactic dehydrogenase I (requiring DPN), although not present in the larva, appeared in the prepupa. Its activity remained relatively constant at a low level throughout the pupal stage and increased in the newly emerged adult. Lactic dehydrogenase II (not requiring DPN) decreased during the change from larva to prepupa and remained relatively constant throughout metamorphosis. Alpha-glycerophosphate I (requiring DPN) increased in activity during the change from larva to prepupa, remained relatively constant throughout the pupal stage, then decreased in the adult. Alpha-glycerophosphate II (not requiring DPN) showed the reciprocal relationship. Isocitric dehydrogenase decreased in activity from the larva to early pupa, remained approximately constant until a final decrease occurred on adult emergence.

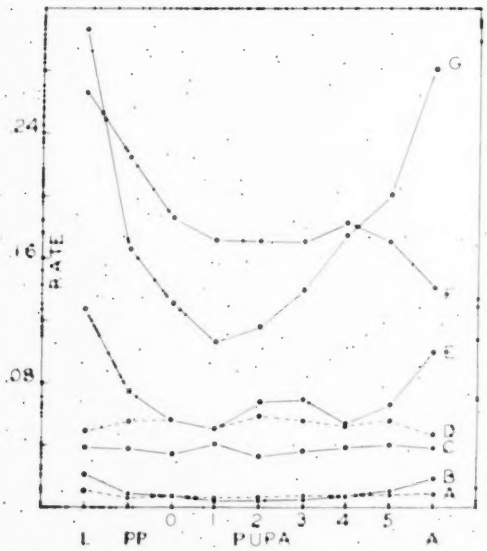


FIG. 1.—Changes in the activity of dehydrogenase enzymes during the metamorphosis of the mealworm. Rate is expressed as 1 time in minutes for 90 percent decoloration of methylene blue. Graph A, glucose dehydrogenase; B, succinic dehydrogenase; C, alcohol dehydrogenase; D, total alpha-glycerophosphate dehydrogenase; E, malic enzyme; F, isocitric dehydrogenase; G, malic dehydrogenase. L, larva; PP, prepupa; A, adult.

The activities of malic and isocitric dehydrogenases were much greater than those of the other enzymes studied. Malic enzyme also showed high activities in the larva and newly emerged adult.

DISCUSSION

The coenzyme requirements of the enzymes tested are similar to those of vertebrates, except for lactic dehydrogenase. In animals this enzyme is DPN-linked, while in plants it does not require DPN (McShan, 1949). The larvae of *Tenebrio molitor* appear to have an enzyme similar to that of plants. However, in the pupa and adult, the addition of DPN increased activity. The mealworm thus appears to have two enzymes capable of oxidizing lactic acid although each of them acts at a very low rate. It is possible that the oxidation of lactic acid without DPN may be accomplished by intracellular symbionts which exist in Tenebrionidae (Steinhaus, 1946) and which, in this laboratory, have been observed in mealworm larvae.

Sacktor (1955) reported that with glucose as a substrate, the addition of either DPN, TPN, or combinations of these cofactors, did not increase the respiration of flight muscle homogenates of the house fly. The present experiments show that with mealworm homogenates, DPN is required for the activity of glucose dehydrogenase. Sacktor (1955) also found that the activity of malic was no greater than that of succinic dehydrogenase. However, his experiments were performed without the addition of DPN. The malic dehydrogenase of mealworm homogenates requires DPN.

Zebe and McShan (1957) studied the oxidation of alpha-glycerophosphate in homogenates of thoracic and leg muscles of a variety of insects. They found two enzymes capable of oxidizing this substrate, one requiring DPN (DGH I) and the other not requiring it (GDH II). The activity of GDH I was much greater than that of GDH II. These results are in agreement with those reported here for homogenates of the mealworm larva.

The observation that choline, beta-hydroxybutyric, formic, and L-glutamic dehydrogenases are absent in mealworm larvae agrees with the findings of Watanabe and Williams (1951) and Sacktor (1955) with insect tissues. Even in mammals, these enzymes are limited to a few

tissues and play only a small role in oxidations (McShan, 1949).

The very high activities of malic dehydrogenase and malic enzyme and the low activity of lactic dehydrogenase are interesting in view of recent discussions on the nature of glycolysis in insect muscle. Gilmour (1941) showed that the amount of lactic acid formed by *T. molitor* larvae subjected to lack of oxygen was not sufficient to account for the glycogen utilized. Barron and Tahmisian (1948) suggested that in the cockroach leg muscle, anaerobic glycolysis resulted in end products other than lactic acid, and Sacktor (1955) stated that his data signify that lactic acid is not an end product of glycolysis in the flight muscle of the house fly. He suggested two possibilities; first, that pyruvate immediately enters the tricarboxylic acid cycle, and second that the later stages in glycolysis as depicted in vertebrate muscle are by-passed in the flight muscle. Zebe and McShan (1957) suggested that the absence of glycolysis from insect muscle could mean that there is little need for anaerobic metabolism because there is never a shortage of oxygen in the tissues. Therefore complete oxidation of substrates is accomplished without the accumulation of intermediates, such as lactic acid. The high activity of malic enzyme coupled with the low activity of lactic dehydrogenase of mealworm homogenates suggest that lactate could not accumulate since the malic enzyme acting anaerobically would reduce the pyruvate directly to malate. (The oxidation of malate to pyruvate by the malic enzyme of insect blood has been shown to be readily reversible by Faulkner, 1956). Malic dehydrogenase would then form oxalacetate from the malate.

Ludwig and Barsa (1956) stated that the activity of succinic dehydrogenase in the mealworm remained constant during the first half and steadily increased during the last half of the pupal stage, whereas in the present work, the activity of this enzyme was found to be U-shaped. In the earlier work, activity was studied spectrophotometrically. This technique measures the reduction of cytochrome *c* with succinate as the substrate. The reaction includes a larger group of enzymes than is included in the Thunberg method. In the present experiments, the activity of succinic dehydrogenase decreased during the pupal stage to a low value of approximately one-fourth, and that of malic to one-third of their values in the larval and adult stages (Table II). This observation, together with the much slower rate of succinic dehydrogenase than those obtained for either malic or malic enzyme indicate that succinic dehydrogenase, in contradiction to the statement made by Ludwig and Barsa (1957), could determine the U-shaped respiratory curve for this species.

REFERENCES CITED

Agrell, I. P. S. 1949. Localization of some hydrogen activating enzymes in insects during metamorphosis. Nature 164: 1039–40.

Barron, E. S. G., and T. N. Tahmisian. 1948. The metabolism of cockroach muscle (*Periplaneta americana*). Jour. Cell. and Comp. Physiol. 32: 57–76.

Faulkner, P. 1956. The 'malic' enzyme in insect blood. Biochem. Jour. 64: 430–6.

Fink, D. E. 1925. Metabolism during embryonic and metamorphic development of insects. Jour. Gen. Physiol. 7: 527–43.

Gilmour, D. 1941. Anaerobic metabolism in the larvae of *Tenebrio molitor* L.: gaseous metabolism and changes in glycogen, sugar, fat, and lactic acid. Jour. Cell. and Comp. Physiol. 18: 93–100.

Green, D. E. The malic dehydrogenase of animal tissue. Biochem. Jour. 30: 2095–110.

Krogh, A. 1914. On the rate of development and CO_2 production of chrysalides of *Tenebrio molitor* at different temperatures. Zeitschr. allg. Physiol. 16: 178–90.

Ludwig, D. 1953. Cytochrome oxidase activity during diapause and metamorphosis of the Japanese beetle (*Popillia japonica* Newman). Jour. Gen. Physiol. 36: 751–7.

Ludwig, D., and M. C. Barsa. 1955. The activity of succinic dehydrogenase during diapause and metamorphosis of the Japanese beetle (*Popillia japonica* Newman). Jour. New York Ent. Soc. 63: 161–5.

1956. Variations in the activity of the succinoxidase system during the development of the mealworm, *Tenebrio molitor* Linnaeus (Coleoptera, Tenebrionidae). Ann. Ent. Soc. America 49: 103–4.

1957. Effects of added substrates and inhibitors on homogenate respiration during the metamorphosis of the mealworm, *Tenebrio molitor* Linnaeus. Ann. Ent. Soc. America 50: 128–32.

McShan, W. H. 1949. Dehydrogenases. In: Respiratory enzymes. Minneapolis: Burgess Publishing Company.

Sacktor, B. 1955. Cell structure and the metabolism of insect flight muscle. Jour. Biophys. and Biochem. Cytol. 1: 29–46.

Steinhaus, E. A. 1946. Insect microbiology. Ithaca: Comstock Publishing Co.

Umbreit, W. W., R. H. Burris, and J. F. Stauffer. 1945. Manometric techniques and related methods for the study of tissue metabolism. Minneapolis: Burgess Publishing Company.

Watanabe, M. I., and C. M. Williams. 1951. Mitochondria in the flight muscle of insects. I. Chemical composition and enzymatic content. Jour. Gen. Physiol. 34: 675–89.

Williams, C. M. 1950. A hormonal-enzymatic mechanism for the control of pupal diapause in the *Cercopia* silkworm. Proc. XVIII Internatl. Physiol. Congr. pp. 517–8.

Wolsky, A. 1938. The effect of carbon monoxide on oxygen consumption of *Drosophila melanogaster* pupae. Jour. Exptl. Biol. 15: 225–34.

1941. Quantitative changes in the substrate-dehydrogenase system of *Drosophila* pupae during metamorphosis. Science 94: 48–49.

Zebe, E. C., and W. H. McShan. 1957. Lactic and alpha-glycerophosphate dehydrogenases in insects. Jour. Gen. Physiol. 40: 779–90.

A Cyanamid Report

MALATHION
FOR DIRECT APPLICATION ON ANIMALS

With newly-granted residue tolerances, malathion can be applied directly to beef cattle, poultry, and swine. This is the result of three years of extensive research in 11 states. The work proved conclusively the safety and usefulness of malathion as a spray for controlling cattle and poultry lice, poultry mites (northern fowl and chicken red mite), and cattle and poultry ticks. In addition, malathion dust may be applied to nests, litter, and floor space. Roost paints using malathion emulsifiable liquid may also be used in poultry houses. In addition to spraying beef cattle with malathion for lice control, rubbing devices incorporating the product have been most effective in suppressing lice and horn flies.

Do not apply malathion to lactating dairy cows, since it has not yet been accepted for this use, nor should it be used on calves under one month of age.

PROTECTANT FOR STORED GRAIN

With newly-granted residue tolerances for malathion on wheat, barley, oats, rice, rye, corn, grain sorghum, and peanuts (post-harvest), grain handlers storing grain have a method of protecting grain from loss to insects. Malathion, either in dust or spray form, *applied to the grain as it is being loaded into bins*, affords protection against confused flour beetle, rice weevil, granary weevil, saw-toothed grain beetle, flat grain beetle, red flour beetle, rusty grain beetle, lesser grain beetle, and Indian meal moth. It is also suggested as a residual wall, floor, and machinery spray in grain elevators, in treating truck beds, box cars, and ships' holds before loading grain. Where Indian meal moth infestations develop, *surface* applications of malathion dusts or sprays at prescribed intervals afford protection.

NEW USES FOR MALATHION ON CROPS

Tolerances have been established on 37 additional crops, including:

Vegetables	Fruits
Asparagus	Bramble family
Carrots and other root crop	Nectarines
Garlic—Leeks—Shallots	Quinces
Several leaf vegetables	Currants
Pumpkins	Gooseberries

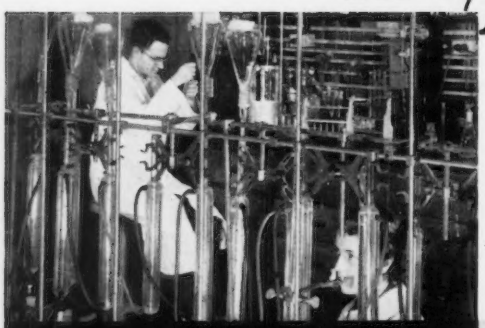
Also, small grains, cotton, mushrooms, peppermint, spearmint, corn and rice. With these additions, malathion is now recommended on 93 crops.

Developers and producers of malathion and parathion

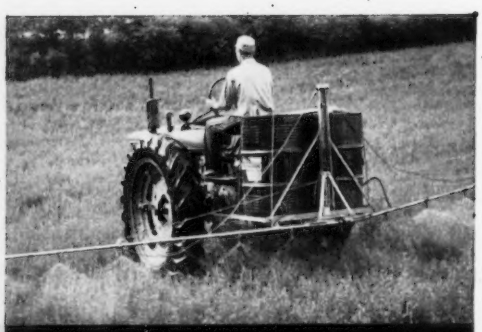
CYANAMID

American Cyanamid Company, Insecticide Department,
30 Rockefeller Plaza, New York 20, N. Y.

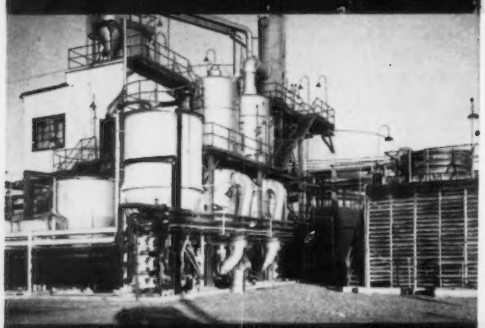
What does it really take to kill insects?



RESEARCH . . . laboratory work that takes many years and millions of dollars



TESTING . . . years of field work, to determine effectiveness, dosages, side effects



PRODUCTION . . . to make commercial quantities available at an economically sound cost

EDUCATION . . . teaching methods of use, gaining confidence and trust

A great deal of work and knowledge goes into the development of insecticides. Once developed, however, they're a priceless defense against the loss of food and fiber, the disease, and the annoyance caused by man's insect enemies. Velsicol Chemical Corporation manufactures five basic insecticides that are thoroughly proven, widely recommended, and extensively used: Heptachlor, Chlordane, Endrin, Parathion and Methyl Parathion. Each of them is rated most efficient for specific types of insect control, and all are available everywhere, in ready-to-use, reasonably priced formulations. If you deal with any phase of insect control, we think you will find technical information about these insecticides highly useful.

NEW! VELSICOL GIBBERELLINS!
Amazing plant growth stimulant. Velsicol's newest contribution to increased agricultural productivity. Extensive research program in progress.

WRITE FOR A BROCHURE OF TECHNICAL INFORMATION, PREPARED BY VELSICOL'S ENTOMOLOGISTS!
HEPTACHLOR • CHLORDANE • ENDRIN • PARATHION • METHYL PARATHION

VELSICOL

VELSICOL CHEMICAL CORPORATION
330 East Grand Ave., Chicago 11, Illinois
International Representative: Velsicol International Corporation, C.A.
P.O. Box 1687 • Nassau, Bahamas, B.W.I.

VC 1126-7108

SUSTAINING ASSOCIATES

ENTOMOLOGICAL SOCIETY OF AMERICA

The firms and institutions listed here are proudly acknowledged as Sustaining Associates of this Society. We commend these Associates to the attention of our members. The effective years shown are as of April 1, 1958.

American Cyanamid Company
Phosphates & Nitrogen Division
30 Rockefeller Plaza
New York 20, New York 1955–58

Birds Eye Division
General Foods Corporation
250 North Street
White Plains, New York 1955–58

California Spray-Chemical Corporation
Executive Offices
Richmond, California and Washington, D. C.
1956–58

Chemagro Corporation
437 Fifth Avenue
New York 16, New York 1955–58

Colloidal Products Corporation
100 Gate 5 Road
Sausalito, California 1956–58

Commercial Enterprises, Inc.
Nursery Division
Newark, New York 1956–58

Dow Chemical Company
American Legion Building
Midland, Michigan 1956–58

E. I. DuPont de Nemours Company, Inc.
Grasselli Chemicals Department
Wilmington 98, Delaware 1955–58

Eastern States Farmers' Exchange, Inc.
26 Central Street
West Springfield, Massachusetts 1956–58

Food Machinery & Chemical Corporation
161 East 42nd Street
New York 17, New York 1955–58

Freeport Sulphur Company
16th Floor, Commerce Building
New Orleans 5, Louisiana 1957–58

General Chemical Division
Allied Chemical & Dye Corporation
40 Rector Street
New York 6, New York 1955–58

Gulf Oil Corporation
Gulf Building
Pittsburgh 30, Pennsylvania 1955–58

Hercules Powder Company
Agricultural Chemicals Division
Naval Stores Department
Wilmington, Delaware 1955–58

Miller Chemical & Fertilizer Corporation
2226 North Howard Street
Baltimore 18, Maryland 1958

Minerals & Chemicals Corporation of America
Menlo Park, New Jersey 1956–58

Monsanto Chemical Company
800 N. 12th Boulevard
St. Louis 1, Missouri 1956–58

S. B. Penick & Company
50 Church Street
New York 8, New York 1955–58

Pennsylvania Farm Bureau Cooperative Association
3609 Derry Street
Harrisburg, Pennsylvania 1955–58

Port Fertilizer & Chemical Company
P.O. Box 337
Los Fresnos, Texas 1955–58

Rohm & Haas Company
222 W. Washington Square
Philadelphia 5, Pennsylvania 1955–58

Shell Chemical Corporation
Agricultural Chemical Sales Division
460 Park Avenue
New York 22, New York 1955–58

Stauffer Chemical Company
Agricultural Chemicals Division
1 East 47th Street
New York 17, New York 1955–58

Swift & Company
Agricultural Chemical Division
Union Stock Yards
Chicago 9, Illinois 1958

Union Carbide Chemicals Company
30 East 42nd Street
New York 17, New York 1956–58

United Fruit Company
Basic Research Laboratories
Upland Road
Norwood, Massachusetts 1955–58

Velsicol Chemical Corporation
330 East Grand Avenue
Chicago 11, Illinois 1955–58

Wisconsin Alumni Research Foundation
Insecticide Testing Laboratory
506 N. Walnut Street
Madison 5, Wisconsin 1958

Woolfolk Chemical Works, Ltd.
P.O. Box 922
Ft. Valley, Georgia 1956–58

TABLE OF CONTENTS

PAGE

BRELAND, OSMOND P.—A Report on *Haemagogus* Mosquitoes in the United States with Notes on Identification (Diptera: Culicidae) 217

ROZEN, JEROME G., JR.—The External Anatomy of the Larva of *Nacerdes malanura* (Linnaeus) (Coleoptera: Oedemeridae) 222

MEDLER, J. T.—A Review of the Genus *Scleroracus* in North America (Homoptera: Cicadellidae) 230

DRAKE, CARL J., AND NICHOLAS A. KORMILEV—Concerning the apterous Aradidae of the Americas (Hemiptera) 241

DAVIS, G. R. F.—Growth and Feeding Behavior of Larvae of *Ctenicera aeripennis destructor* (Brown) (Coleoptera: Elateridae). III. Effects of Seeds of Crested Wheatgrass, Bromegrass, and Rape 248

PATHAK, M. D., AND REGINALD H. PAINTER—Differential Amounts of Material Taken up by Four Biotypes of Corn Leaf Aphids from Resistant and Susceptible Sorghums 250

BARKER, ROY J., AND B. H. ALEXANDER—Acid and Alkaline Phosphatases in House Flies of Different Ages 255

WILLIS, EDWIN R.—The Use of Artificial Heat to Induce Mosquitoes to Feed on Cold-Blooded Animals 257

KAMAL, ADEL S.—Comparative Study of Thirteen Species of Sarcosaprophagous Calliphoridae and Sarcophagidae (Diptera). I. Bionomics 261

CALLAHAN, PHILIP S.—Behavior of the Imago of the Corn Earworm, *Heliothis zea* (Boddie), with Special Reference to Emergence and Reproduction 271

BECK, STANLEY D., C. A. EDWARDS, AND JOHN T. MEDLER—Feeding and Nutrition of the Milkweed Bug, *Oncopeltus faciatus* (Dallas) 283

FOOTE, RICHARD H.—The Genus *Euarestoides* in the United States and Mexico (Diptera, Tephritidae) 288

TARSHIS, I. BARRY—A Preliminary Study on Feeding *Ornithodoros savignyi* (Audouin) on Human Blood Through Animal-Derived Membranes (Acarina: Argasidae) 294

HOUSE, H. L., AND J. S. BARLOW—Vitamin Requirements of the House Fly, *Musca domestica* L. (Diptera: Muscidae) 299

STEYSKAL, GEORGE C.—Notes on the Richardiidae, with a Review of the Species Known to Occur in the United States (Diptera, Acalyptratae) 302

LUDWIG, DANIEL, AND MARY C. BARSA—Activity of Dehydrogenase Enzymes During the Metamorphosis of the Mealworm, *Tenebrio molitor* Linnaeus 311